ECOLOGICAL STRATIFICATION IN THE PLEISTOCENE CORAL REEFS OF THE KENYA COAST

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ABSTRACT. Ecological succession on small patch reef structures can be studied by employing the concept of ecological stratification. The component corals of a patch are divided into two basic categories, the B or C horizons (or strata). The former category represents the initial colonizers (or pioneers) on a soft substrate, and the latter the subsequent colonizers. The potential exists for studying the later stages of succession by finely subdividing the C horizon. Detailed mapping of vertical sections through patch reefs in the Pleistocene reef limestones of the Kenya coast provided stratification analyses in a variety of back-reef environments. Massive *Porites* proved to be the commonest B horizon coral throughout the region studied, and clearly was of fundamental importance in patch reef formation. Massive faviids and mussids were less frequent early colonizers. The most important C horizon corals were encrusting *Montipora* (in more open water areas), encrusting *Cyphastrea* (in quieter, deeper water areas), and tiny domes and patches of massive *Favia*. Many corals may be much more specialized in their habitat requirements than has previously been recognized. The principal coral types within the back-reef patches of the Kenya Pleistocene reef consistently adopt distinctive three-dimensional growth forms within either B or C horizons, and it is argued that they must have partitioned at least part of the available habitat space. Ecological stratification is a useful tool for determining the nature and extent of habitat resource partitioning by scleractinian corals.

PALAEONTOLOGICAL studies of ecological succession have now advanced beyond the stage of purely qualitative descriptions. Intensive sampling techniques have been developed that permit not only the detailed elucidation of vertical faunal trends, but also the quantitative analysis of changes in parameters such as species abundance and diversity through time (e.g. Alberstadt and Walker 1976; Bretsky and Bretsky 1975, 1976; Walker and Alberstadt 1975; Walker and Parker 1976; Rollins, Carothers and Donahue 1979). In fossil reef studies, a particularly promising line of research lies in the application of quadrat survey techniques to the study of vertical sections. Although relatively time-consuming, such techniques permit far more detailed analysis of successional trends than has hitherto been possible (e.g. Scott and Brenckle 1977; Crame 1980). However, it is becoming apparent that use of such vertical quadrats is essentially restricted to areas of thick, continuous reef framework. In Pleistocene reef studies, for example, it has been found that a quadrat usually has to measure at least 2–3 m (width) by 1·5–2·0 m (height) for meaningful faunal trends to be detected (Crame 1977, 1980). On small, spherical reef structures, such as patches and knolls, vertical analysis by quadrat survey techniques becomes inappropriate, for here growth has often been as much outward (in all directions) as it has been upward. Clearly, an alternative strategy is required for the study of succession in small knoll and patch reef areas.

In an attempt to apply some of the field-survey techniques of plant ecology to the study of recent coral assemblages, Rosen (1971, 1972) showed that corals could often be grouped into distinct strata (or ecostrata). Three principal strata can be identified in reef-associated assemblages (Rosen 1971, p. 148; see also Pichon 1978, p. 223). The first (Stratum A) consists of all the soft substrates normally developed on reefs (principally sands) and Stratum A organisms are those that inhabit sands infaunally (i.e. not normally applicable to corals). Stratum B corals are those which live on the sands and in turn provide a substrate for corals of the C stratum. In practice, Rosen (1971, 1972) found it convenient to subdivide the B stratum into various size categories (B_1, B_2, etc.) and the C stratum into

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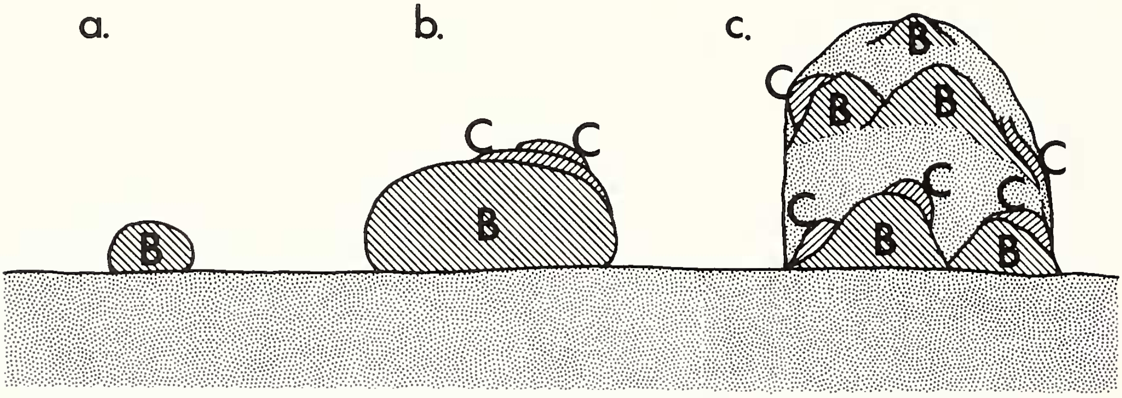
subunits (C_1, C_2, etc.) that represented successive phases of subsequent colonization. Although certain coral species appear to be just as common to either the B or C strata, others were found to be definitely restricted to one or the other (Rosen 1971, 1972): some forms showed a marked preference for colonizing soft substrates (i.e. B stratum) and others only ever appeared uncrusting or attached to a hard substrate (i.e. C stratum). Indeed, in certain reef environments (especially those that may be loosely termed, 'back-reef'), there appear to be distinct substrate associations of B and C strata corals (Rosen 1971, 1972).

This concept of ecological stratification would seem to be particularly amenable to the analysis of small patch reef structures, for the initial colonizers in a patch will belong to the B stratum and later colonizers to the C. In the simplest case a patch could be formed out of a single coral that has grown across a bare substrate: as the latter is usually soft (colonization of intertidal benches will not be considered in this study), this single component coral will be classified as belonging to the B stratum (text-fig. 1*a*). Other coral types may subsequently colonize an initial B, and in time a more complex patch composed of both B and C strata corals could be built up (text-fig. 1*b*). As patches increase in size they generally incorporate loose sediment into their structure and it is possible for the B stratum to become re-established: indeed, many larger patches are often composed of several distinct generations of B and C strata (text-fig. 1*c*). In theory it is possible to subdivide these strata, and the finer the divisions made, the more precise the final reconstruction of the stages of patch development will be. However, it was found that the resolution of fossil patches into a series of discrete substrata posed a number of problems. In particular, it often proved extremely difficult to determine the true order of appearance of C strata corals, for their may be no reliable criteria for establishing whether or not widely separated corals were contemporaneous. Another problem is that in some instances the C strata could have developed while at least part of the B stratum was still alive. It was therefore decided not to attempt a refined subdivision of the component B and C strata in each of the patches studied. Instead, attention was focused on resolving the constituent corals of each patch into either of two basic categories, the B or C strata. Such a resolution into undifferentiated B and C strata may, in some cases, lead to a loss of definition, but nevertheless it still reflects two fundamental stages in patch formation; initial (B stratum) and subsequent (C stratum) colonization. Obviously, the technique is most applicable to the study of small, simple structures, but the results here indicate that stratification analysis also reveals the basic steps in the development of structures measuring up to several metres in their maximum dimensions.



TEXT-FIG. 1. Three examples of ecological stratification in back-reef coral patches: *a*, a single B stratum massive coral that has grown across a sands substrate; *b*, a larger patch with later-colonizing C strata corals on top of an initial B; *c*, a complex patch composed of several distinct generations of B and C strata corals. N.B. In this study the term horizon is used instead of stratum (see text).

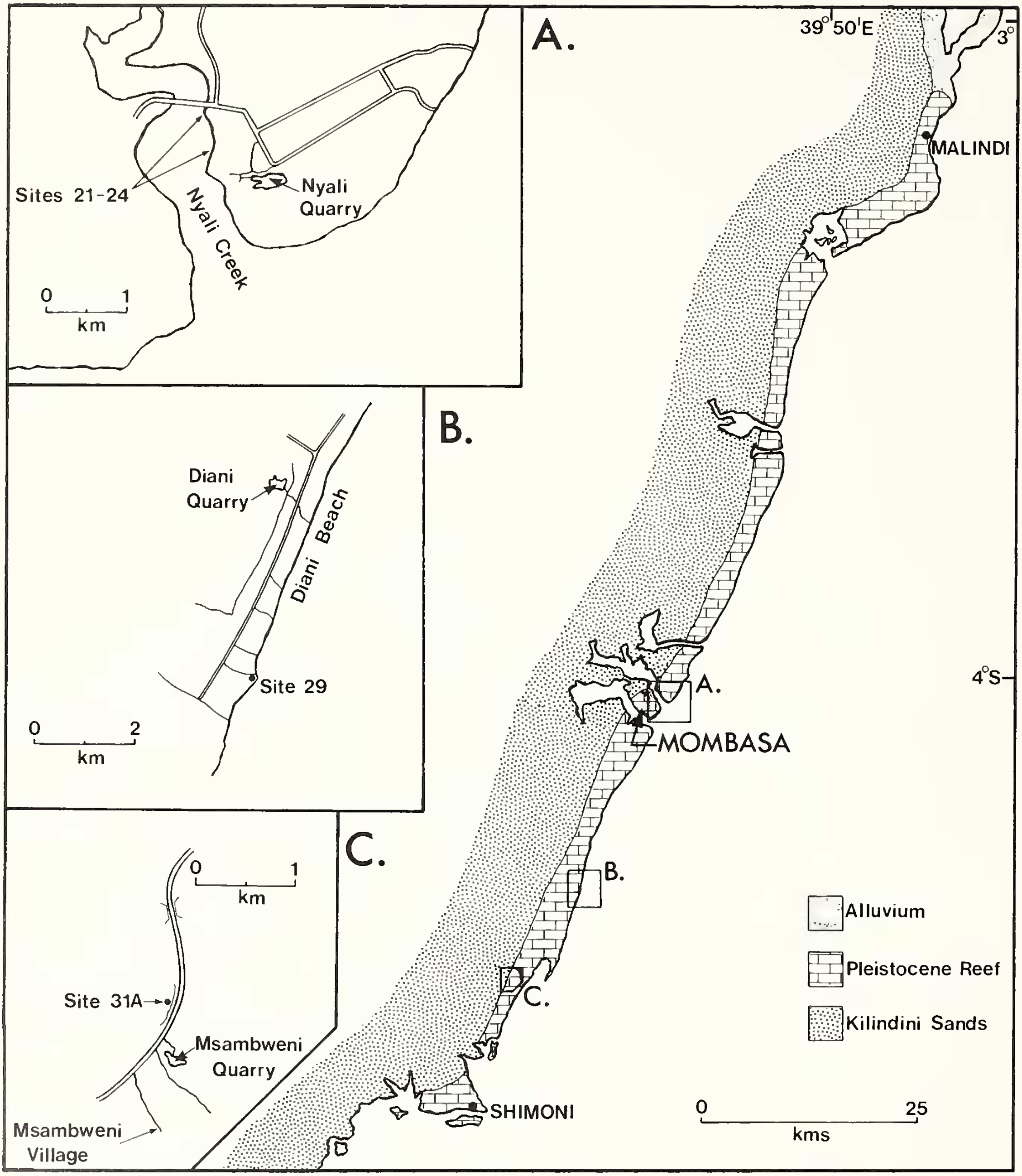
Although strata and stratification are widely used botanical terms, they cannot be employed in geological studies without causing some degree of ambiguity. Geological strata could become confused with ecological strata. Thus it is necessary to change the terminology, and in this study the term horizon has been substituted for stratum (i.e. B horizon, C horizon, etc.). Also, the stratification scheme developed for the study of coral assemblages is not strictly analogous to the stratification normally associated with plant assemblages. In the latter case all the strata originate from the same substrate level and are strictly contemporaneous, but coral strata (horizons) are interdependent and essentially sequential in their development. Stratification similar to that seen in plant assemblages could, of course, occur in coral assemblages, but this remains a phenomenon which can only be fully investigated on Recent reefs. An important by-product of this method of analysis is that the data acquired by grouping corals into discrete horizons can be directly applied to an investigation of the spatial resource requirements of patch reef corals. It will become apparent below that for each coral in a patch its substrate, size, and growth form are determined. Data from a whole series of patches can be pooled and an assessment made of whether the principal coral species have consistently occupied the same type of substrate and adopted the same three-dimensional growth forms. Hence it may be possible to determine whether the principal coral types have effectively partitioned the available habitat space on patch reefs.

FIELD AREA AND METHODS

The Pleistocene reef limestones of the Kenya coast are well exposed in cliff, quarry, and road-cut sections between Malindi and Shimoni (text-fig. 2). At least part of the reef deposits are underlain by the Pleistocene Kilindini Sands, and it is thought they can largely be dated as last Interglacial (*c.* 120 000 years BP) (Braithwaite, Taylor and Kennedy 1973, p. 333; Crame 1977). Stratigraphical investigations of the reef have yet to be completed, but it is likely that all the exposures described in this study are part of the main reef limestones and broadly contemporaneous. Facies relations within the reef deposits are complex and as yet only a very general reconstruction of the Pleistocene reef can be attempted. There is some evidence to suggest that remnants of the seaward extremities of the reef are preserved in the outermost headlands, but it would seem that the vast majority of the present-day exposures are through what was an extensive back-reef region. Thick frame assemblages occasionally developed in this region but over most of it there were only small, isolated coral mounds and knolls (Crame 1977, figs. 57, 79, and 80; 1980, text-fig. 2). Available evidence suggests greater equivalence with the deeper-water areas of present-day reef flats than with true lagoons (see discussion section, below).

Patch reefs, *sensu lato*, are generally regarded as any isolated coral structure growing up from the floor of an atoll or shelf lagoon. Their shape is very variable and in size they can measure up to tens (or even hundreds) of metres across. Some authors have differentiated between patch reefs which reach the surface and knoll reefs which do not (e.g. Chevalier 1973), and others have attempted morphological or genetic classifications (e.g. Maxwell 1968; Marszalek *et al.* 1977; Jones 1977; Brown and Dunne 1980). In the Kenyan Pleistocene reef the vast majority of the patches are small, nearly all being less than 4 m in width by 4 m in height: larger, complex structures (up to 20 m across) were occasionally found, but these are the exceptions rather than the rule. All grades of complexity from single B horizon to multi-generation B and C horizon patches are present.

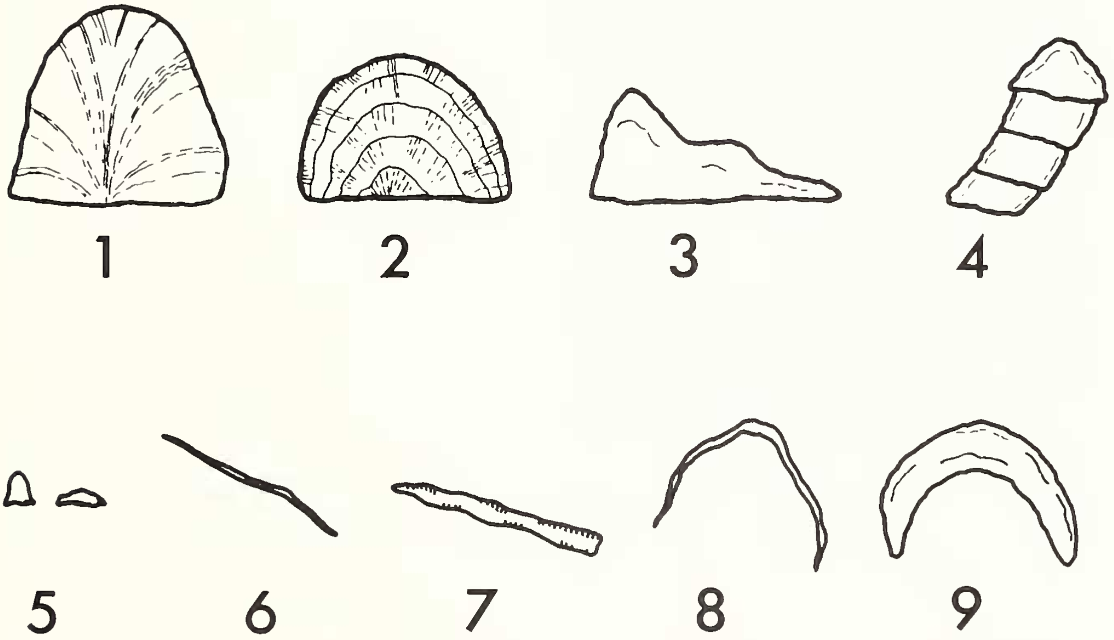
Vertical sections through back-reef patch facies were studied at a number of sites from Malindi to Shimoni (text-fig. 2). From this initial reconnaissance, three areas were selected for intensive study: (i) Nyali Creek (Sites 19–24); (ii) Nyali Quarry (Site 26); and (iii) the Diani-Msambweni area (Sites 29–31) (text-fig. 2). Sedimentary and faunal evidence suggest that slightly different environmental conditions prevailed in each of these areas, and there are corresponding variations in both the nature and sequential development of their respective patch reef faunas. At each site within these three areas a series of adjacent patches were mapped in detail at a scale of 1 : 10 (using the technique of vertical quadrat analysis given in Crame 1980, p. 5). Sedimentary structures in the inter-reef sediments were also mapped, and as before care taken to distinguish any corals which may not be *in situ*. The maps



TEXT-FIG. 2. A simplified geological map of the Kenya coast. Inset A shows the location of Nyali Creek and Nyali Quarry, and insets B and C the position of Diani and Msambweni Quarries. N.B. Nyali Quarry = Site 26, Diani Quarry = Site 30, and Msambweni Quarry = Site 31.

were analysed by splitting each patch into its component B and C horizon faunas. A coral was assigned to the B horizon if it rested on what was a soft substrate and the C horizon if it had obviously grown on a hard substrate (e.g. another coral, encrusting calcareous algae or a rubble fragment). Many B horizon corals may of course have initially developed on a tiny hard substrate patch (such as a shell or coral fragment), but they clearly subsequently grew across a soft substrate. The B horizon in this study includes three basic types of coral: initial colonizers that formed cores to patches, corals that became established on sediment incorporated into large patches, and isolated corals that were not subsequently colonized. The C horizon comprises those corals that colonized an initial B, those that colonized an earlier C, and a number of small colonies that grew on isolated rubble fragments and patches of encrusting calcareous algae. It should be emphasized that although the maps represent planar sections, most of the patches studied were at least partially exposed in three dimensions. The tops and bottoms of individual corals could usually be traced in several directions and the true relationships with adjacent colonies established. The small number of colonies that could only be tentatively assigned to either the B or C horizons were excluded from the subsequent analyses.

For each coral within a patch an estimate was made of both its growth form and size. Nine growth-form categories were established to cover the principal coral types encountered, and these have been arranged in an approximate morphological series grading from massive to encrusting types (text-fig. 3; see also Tables 2, 5, and 7). As will become apparent below, very few branching corals were found at any of the sites investigated. Estimates of colony sizes were made using the technique previously employed in the analysis of vertical quadrats (Crame 1980, p. 7). The outline of a coral colony, as projected on to the plane of the paper, was taken to represent a vertical section through it,



TEXT-FIG. 3. The scheme of coral growth forms used in this study. *Key*: 1. Doming-Massive; 2. Dome formed out of Successive Encrusting Layers; 3. Massive-Irregular; 4. Massive Tubes and Pillars; 5. Tiny Domes and Encrusting Patches; 6. Platy-Encrusting, Thin; 7. Platy-Encrusting, Thick; 8. Doming-Encrusting, Thin; 9. Doming-Encrusting, Thick. The boundary between thin and thick encrusting colonies has been placed at a maximum colony thickness of 35 mm.

and an estimate was made of the area of this shape using a simple grid-overlay method. The resulting figure, the number of squares on the grid occupied by a planar section through the colony, is termed the Importance Value of the coral: a value of 1 corresponds to an area of 25 cm^2, of 5 to 125 cm^2, and so on. Thus, the substrate, growth form and size of each coral present within a patch is determined. For a series of adjacent patches these results can be combined to give a comprehensive outline of the process of ecological stratification within a given area.

It was not always possible to identify corals accurately to the species level. In a number of instances the fine surface details upon which accurate identifications depend have either been lost (through abrasion or diagenetic solution) or obscured, and certain closely related species have had to be grouped together. The scheme of coral groupings used here is based on that given in a previous study (Crame 1980, p. 36).

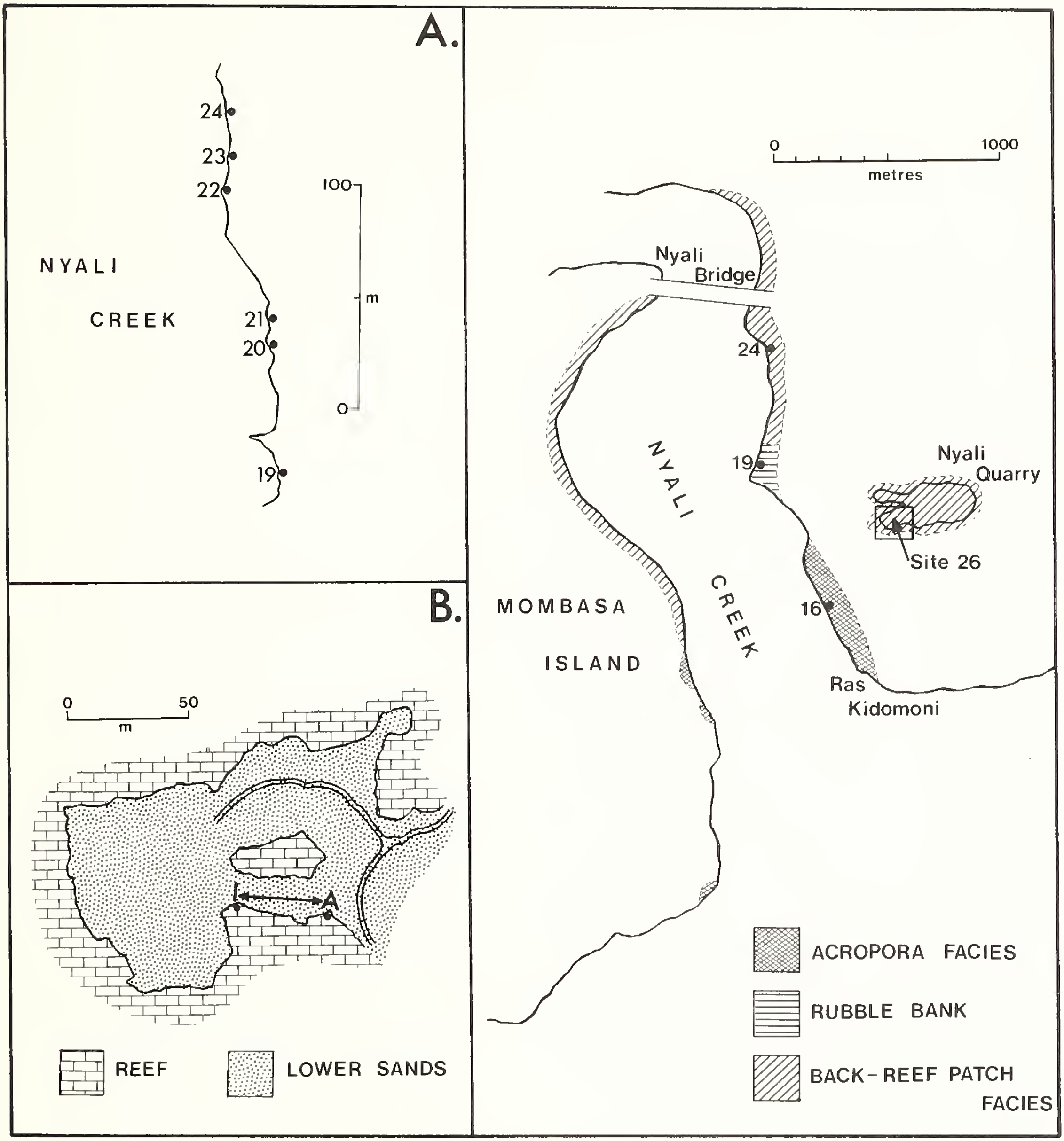
DETAILED STRATIFICATION DATA

The Nyali Creek

Small to medium-sized coral patches are well exposed in cliffs (6–8 m high) along the eastern bank of Nyali Creek, between Ras Kidomoni and Nyali Bridge (text-figs. 2 and 4). They developed in what was a rubbly back-reef area lying to the lee of an extensive bank of branching coral. Quiet water conditions must have existed in this region, but there were evidently regular incursions of rubbly material. A prominent bank of stagshorn *Acropora* at Site 16 passes inwards into a distinctive branching rubble facies at Site 19 (text-fig. 4). The lower levels of the cliffs in the vicinity of this site are composed of a thick mesh of broken coral branches (generally up to 3 cm in diameter) which appear at first sight to be entirely loose and random in orientation. However, closer inspection reveals patches of *in situ* framework and it is believed that this area was the site of a wide bank of branching coral, mainly composed of *Porites* sp. gp. 1. Other corals which managed to become established on this thick mesh of branching coral include a small number of large, massive *Porites* (at low levels in the cliff), several smaller *Porites* and faviids, and some thick-branching colonies of *Acropora palifera* (Lamarck). The bank of branching material is still present at Site 20 (text-fig. 4) where it supports several very large colonies of 'organ-pipe' *Goniopora* (= *G*. sp. gp. 2, a grouping of large, thick-branching species of *Goniopora*). Between Sites 20 and 21 (text-fig. 4) there is an abrupt change in facies as the thick mesh of branching coral is replaced by an assemblage of isolated coral patches set in a matrix that has both fine- and coarse-grained components. The patches occur at all levels in the cliff and are composed of a variety of coral types. They are typically set in a fine, sandy matrix that in places becomes almost silty in texture. Scattered through this fine matrix are coarse rubbly fragments that have been derived from both branching and platy coral types. The finer grained matrix probably represents the more normal conditions of slow sedimentation in a quiet water area. Periodically, however, there were large influxes of rubble which must have swamped much of the substrate and considerably stirred up the sea floor. The most marked of these periodic influxes formed the distinct layers of rubble that can be seen at several levels in the cliff face. Small patches at Sites 22 and 23 (text-fig. 4) are again set in a sandy-rubbly matrix and it is likely that their development was considerably impeded by the frequent incursions of rubble. However, rubble is much less in evidence at Site 24 (text-fig. 4), and here there are a number of large *Porites* patches set in a fine, sandy-silty matrix. Indeed, the extensive areas of fine sediment suggest that quiet-water conditions may have prevailed in this area for long periods of time.

Ecological stratification at Sites 21–24. Detailed investigations of the patch reef faunas in the Nyali Creek were made at four sites (Sites 21–24, text-fig. 4).

Site. 21 (area of study plot, 2·5 m (horizontal) by 1·5 m (vertical)) (text-fig. 5). One large patch dominates this study area. It is centred on a large, thick-branching colony of *Goniopora* (*G*. sp. gp. 2), which clearly belongs to the B horizon (text-fig. 5). Fine sediment and rubble accumulated in the central region of this colony and eventually a second B horizon coral, a *Porites* sp. gp. 2, became established (text-fig. 5). Several small C horizon



TEXT-FIG. 4. A facies and locality map for the Nyali region. Inset A shows the location of Sites 19–24 along the eastern bank of Nyali Creek. Inset B is a sketch-geological and locality map of the south-western embayment of Nyali Quarry (Site 26) showing the positions of patches A–I.

TEXT-FIG. 5. Part of the study plot at Site 21. *Key*: 1. *Goniopora* sp. gp. 2 (B horizon); 2. *Porites* sp. gp. 2 (B); 3. platy-encrusting faviids on rubble fragments (C); 4. *Echinopora gemmacea* (C); 5. *Goniastrea pectinata* (C). Horizontal and vertical grid interval: 0·5 m.

corals subsequently grew on this large *Porites* colony, but very few developed on the initial *Goniopora* (text-fig. 5). There is one other prominent B horizon *Porites*, and a number of tiny encrusting C horizon corals that grew on the larger rubble patches. Analysis of this fauna into B and C horizons (Table 1) shows that the former is dominated by a small number of large *Porites* colonies and a single large colony of *Goniopora* sp. gp. 2. All the C horizon corals are very much smaller than the B horizon ones, and nearly all have encrusting growth forms. There are two tiny domes of *Favia* sp. gp. 1, but all the other corals are encrusting forms of types such as *Porites*, *Goniastrea*, *Cyphastrea*, and *Merulina* (Table 1).

Site 22 (2·5 × 2·0 m). A single, large B horizon colony of *Porites* sp. gp. 2 forms the core of a small mound at the base of this site. Alternate layers of fine sediment and coarse rubbly material subsequently accumulated over this mound, but no other large colonies became established. The B horizon also contains a number of small to medium-sized domes of *Porites*, *Platygyra*, and *Favia*, as well as several small encrusting colonies (Table 1). However, stratification is very limited in this area and there are only a few very small encrusting domes and patches in the C horizon (Table 1).

Site 23 (5 × 2 m) (text-fig. 6). The two prominent mounds at the base of this study plot clearly have composite coral-rubble cores. They are composed of a mixture of *in situ* B and C horizon corals, platy and branching fragments, and sediment (text-fig. 6). Alternating fine and rubbly layers were deposited over these mounds and later corals became established on both soft and hard substrates. However, a noticeable feature of this study area is that there are no large corals at any level (text-fig. 6). As in the higher levels at Site 22, it would appear that the frequent incursions of rubble fragments must have prevented the development of extensive coral colonies. Small to medium-sized massive colonies of *Porites* sp. gp. 2, *Favia* sp. gp. 1, *Goniastrea retiformis* (Lamarck) and *Symphyllia* sp., together with thick-encrusting colonies of *Cyphastrea*, are the most important B horizon corals (Table 1). An interesting feature shown by a number of these colonies is their adoption of distinctly 'tubular'

TABLE 1. Principal B and C horizon corals at Sites 21–24. N—number of colonies; Total IV—total importance values.

SITE 21

Principal B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	4	444·00
cf. *Porites* sp. gp. 2	1	26·00
Goniopora sp. gp. 2	1	370·00
	6	840·00
Principal C horizon corals		
Porites sp. gp. 2	4	9·75
Favia sp. gp. 1	3	4·50
Goniastrea pectinata	2	9·00
Cyphastrea micropthalma	3	1·50
Merulina sp.	3	1·50
	15	26·25

SITE 22

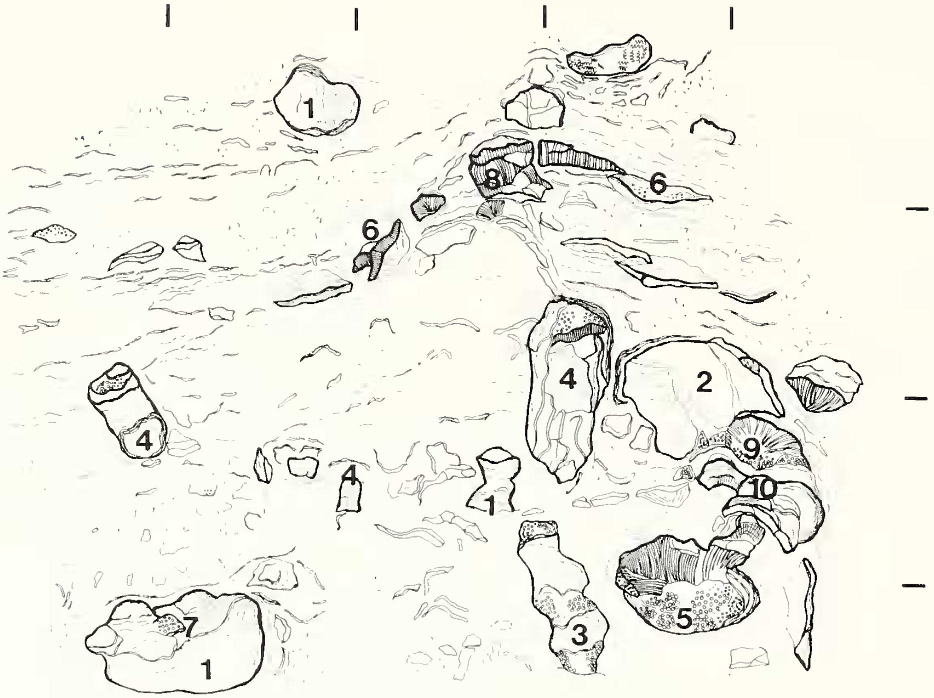
Principal B horizon corals	*N*	*Total IV*
Montipora sp.	1	2·00
cf. *Montipora* sp.	2	10·00
Porites sp. gp. 2	7	118·00
Favia sp. gp. 1	2	2·00
Platygyra sp.	1	9·00
cf. *Cyphastrea* sp.	1	5·00
	14	146·00
Principal C horizon corals		
Porites sp. gp. 2	1	6·00
Favia sp. gp. 1	2	6·50
cf. *Favia* sp. gp. 1	1	8·00
Cyphastrea sp.	3	5·50
cf. *Cyphastrea* sp.	2	1·25
Echinopora sp.	2	3·00
	11	30·25

SITE 23

Principal B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	4	71·00
cf. *Porites* sp. gp. 2	1	16·00
Favia sp. gp. 1	1	28·00
Goniastrea retiformis	1	21·00
Cyphastrea micropthalma	2	12·00
cf. *Cyphastrea* sp.	2	9·00
Galaxea fasicularis	2	6·00
Symphyllia sp.	1	5·00
	14	168·00
Principal C horizon corals		
Montipora sp.	4	7·00
cf. *Montipora* sp.	4	11·00
cf. *Pavona* sp.	2	3·00
Agariciella ponderosa	1	5·00
Porites sp. gp. 2	3	32·00
cf. *Porites* sp. gp. 2	1	9·00
Favia sp. gp. 1	7	18·50
Goniastrea sp.	2	8·25
Platygyra lamellina	1	13·00
Cyphastrea sp.	4	12·50
Galaxea fascicularis	1	6·00
	30	125·25

SITE 24

Principal B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	18	2105·00
Plesiastrea sp.	1	6·00
Favia sp. gp. 1	1	2·00
Goniastrea pectinata	1	2·00
Leptastrea sp.	1	12·00
Cyphastrea sp.	3	49·00
	25	2176·00
Principal C horizon corals		
Montipora sp.	5	17·75
Pachyseris sp.	2	30·25
Porites sp. gp. 2	5	278·00
Favia sp. gp. 1	15	5·00
Goniastrea pectinata	8	36·00
G. cf. *pectinata*	3	16·00
Platygyra sp.	3	50·50
cf. *Hydnophora* sp.	1	8·00
Leptastrea sp. gp. 1	2	17·00
Cyphastrea sp.	17	15·25
Echinopora sp.	3	18·00
Symphyllia sp.	1	10·00
	65	501·75



TEXT-FIG. 6. One of two prominent mounds at the base of the study plot at Site 23. *Key*: 1. *Porites* sp. gp. 2 (B horizon); 2. *Porites* sp. gp. 2 (? B); 3. 'tubular' *Goniastrea retiformis* (B); 4. 'tubular' *Cyphastrea* sp. (B); 5. *Favia* sp. gp. 1 (B); 6. *Echinopora* sp. (? B); 7. *Favia* sp. gp. 1 (C); 8. *Platygyra* sp. (C); 9. *Galaxea fascicularis* (C); 10. *Montipora* sp. (C). Horizontal and vertical grid interval: 0·5 m.

growth forms. These tubular coralla, which measure up to 50 cm in height and 30 cm in width, probably reflect a strategy to grow quickly up and away from a muddy substrate. They are particularly well seen in several thick-encrusting colonies of *Cyphastrea* (some of which are truly hollow) and in a single doming-massive colony of *G. retiformis* (text-fig. 6). Thick, encrusting corals are very much in evidence in the C horizon: *Porites* sp. gp. 2, *Montipora*, and *Cyphastrea* are the commonest types, but there are also encrusting colonies of *Platygyra*, *Goniastrea*, and *Gardineroseris* (Table 1). The other distinctive feature of the C horizon is the presence of a number of small domes and patches of *Favia* sp. gp. 1 (Table 1).

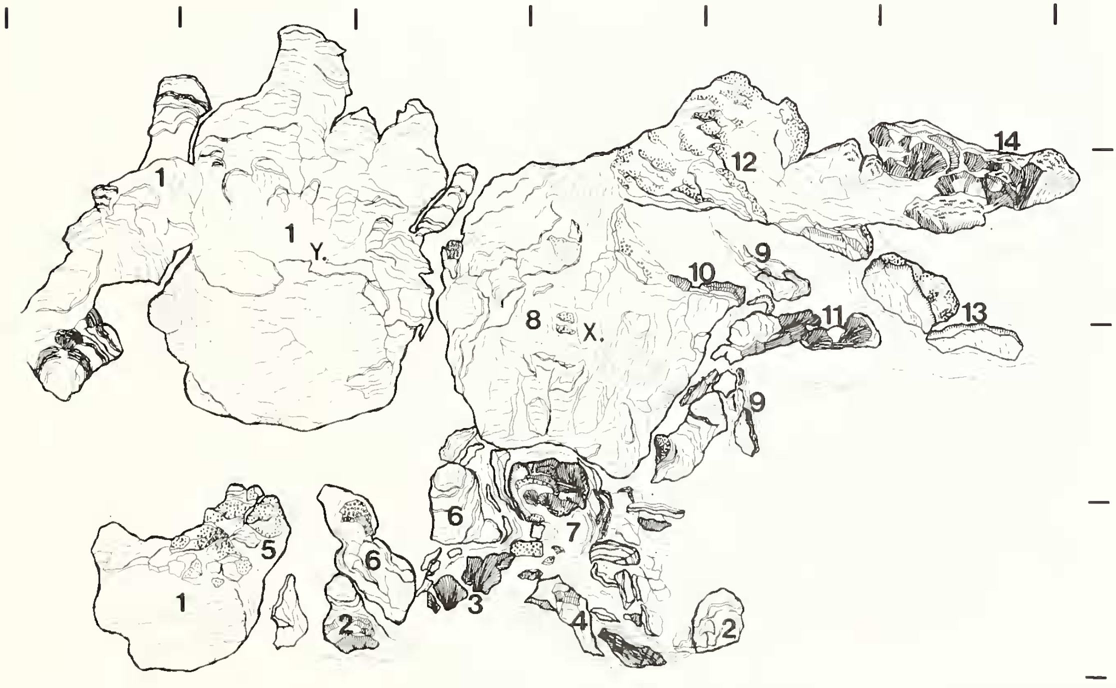
Site 24 (8 × 4 m) (text-fig. 7). Large patches are well exposed at this site and it was possible to make a detailed analysis of patch development over an extensive area. Within the delimited study plot large patches occur in three main clusters of approximately equal size (one of which is shown in text-fig. 7). Smaller patches occur between the main clusters and there are numerous isolated occurrences of small B and C horizon corals. Analysis into B and C horizons (Table 1) shows that the patches are predominantly based on large B horizon colonies of *Porites* sp. gp. 2. Fifteen very large *Porites* colonies occur within the study area: two have importance values greater than 200, and a third a value of over 700. Other B horizon corals include four small faviids and three 'tubular' colonies of *Cyphastrea* (text-fig. 7 and Table 1).

Stratification is altogether more extensive at this site than at any of the others previously described, and a number of large colonies are present in the C horizon (Table 1). There are several large doming-massive colonies of *Porites* sp. gp. 2, *Platygyra*, and *Leptastrea* sp. gp. 1 (a group comprised principally of *L. purpurea* Dana and *L. transversa* Klunzinger), as well as large doming-encrusting types such as *Goniastrea pectinata* (Ehrenberg) and *G. retiformis*. The more extensive stratification at this site is well illustrated by the patch centred on colony X (text-fig. 7). This patch initiated with the development of a massive B horizon *Plesiastrea* and a thick-encrusting

Echinopora (? B horizon, text-fig. 7). A doming-massive *Leptastrea* sp. gp. 1 grew on the initial mound and this was in turn followed by a very large doming-massive *Porites* sp. gp. 2 (colony X). Subsequent C horizon corals based on this C horizon *Porites* include *Echinopora*, *Symphyllia*, *Leptastrea* sp. gp. 1, and *Platygyra* (text-fig. 7). However, it should be pointed out that such extensive stratification is rather rare, and an adjacent massive *Porites* colony (colony Y, text-fig. 7) supports no C horizon at all. Among the other C horizon corals, there are several large encrusting colonies of *Pachyseris* and *Echinopora*, and many small encrusting patches of *Favia* sp. gp. 1, *Cyphastrea* and *Echinopora*.

Summary of ecological stratification at Sites 21–24

The results from Sites 21–24 are summarized in Table 2, which shows the numbers of B and C horizon corals in each importance value and growth-form category. Using this table, it is possible to draw a number of general conclusions about the changes in species composition, colony size, and growth form during patch development in the Nyali Creek. There is a considerable reduction in mean coral colony size from the B to C horizons. Whereas 49% of the B horizon colonies have an importance value of 11 or greater (i.e. medium or large categories), the corresponding figure for the C horizon is only 8%. In fact, nearly 60% of the C horizon corals fall within the lowest (0–1) importance value category (Table 2). It is also obvious from Table 2 that there are marked changes in growth form between the two horizons. The majority (80%) of the B horizon corals have a growth form within one of the first four categories in Table 2 (i.e. large, massive forms), but the equivalent figure for the same categories in the C horizon is only 12%. Nearly all the latter have growth forms within categories 5–9 (i.e. tiny domes, and the platy- and doming-encrusting forms) (Table 2). Thus, there is general trend



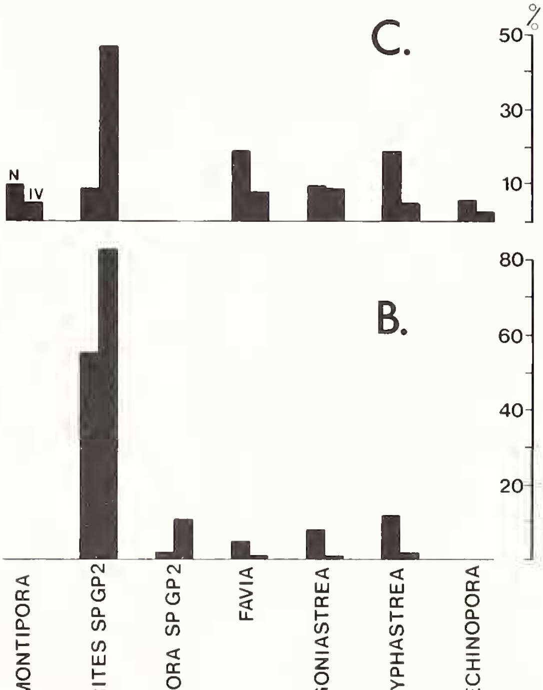
TEXT-FIG. 7. Part of the study plot at Site 24. *Key*: 1. *Porites* sp. gp. 2 (B horizon); 2. 'tubular' *Cyphastrea* sp. (B); 3. *Plesiastrea* sp. (B); 4. *Echinopora* sp. (? B); 5. Small domes and patches of *Favia* sp. gp. 1 and *Goniastrea* sp. (C); 6. *Montipora* sp. (C); 7. *Leptastrea* sp. (C); 8. *Porites* sp. gp. 2 (C); 9. *Cyphastrea* sp. (C); 10. *Echinopora* sp. (C); 11. *Symphyllia* sp. (C); 12. *Leptastrea* sp. gp. 1 (C); 13. *Goniastrea* sp. (? B); 14. *Platygyra* sp. (C). Horizontal and vertical grid interval: 0·5 m. For explanation of colonies marked X and Y see text.

TABLE 2. Summary of ecological stratification at Sites 21–24. The table shows the number of B and C horizon occurrences of each coral species within the various importance value and growth-form categories. Approximate size equivalence of the importance value categories: 0–1, very small; 2–10, small; 11–20 and 21–50, medium; 51–100, large; 100+, very large. Growth form categories: 1. Doming-Massive; 2. Dome formed out of Successive Encrusting Layers; 3. Massive-Irregular; 4. Massive Tubes and Pillars; 5. Tiny Domes and Encrusting patches; 6. Platy-Encrusting, Thin; 7. Platy-Encrusting, Thick; 8. Doming-Encrusting, Thin; 9. Doming-Encrusting, Thick. The boundary between thin- and thick-encrusting colonies has been placed at a maximum colony thickness of 35 mm. N.B. the growth forms of *Goniopora* sp. gp. 2, *Galaxea fascicularis*, and *Lobophyllia* fall outside this scheme.

	IMPORTANCE VALUES								GROWTH FORMS								
	0–1	2–10	11–20	21–50	51–100	101–200	201–300	300+	1 Dom.-mass.	2 Dom.-encr. lyrs.	3 Mass.-irreg.	4 Mass.-tub. & pill.	5 Tiny domes & pat.	6 Platy-encr. thin	7 Platy-encr. thick	8 Dom.-encr. thin	9 Dom.-encr. thick
B HORIZON																	
Montipora sp.		1								1							
cf. *Montipora* sp.		2													2		
Pavona sp.	1															1	
Pachyseris sp.	1													1			
Porites sp. gp. 2	1	7	4	10	6	3		3	24		4	5			1		
Goniopora sp. gp. 2								1									
Plesiastrea sp.		1							1								
Favia sp. gp. 1	1	1		1					3								
Goniastrea retiformis				1								1					
G. pectinata	2	2								2			1				1
Platygyra sp.		1							1								
Leptastrea sp.			1							1							
Cyphastrea micropthalma		2										2					
C. sp.		2		1						3							
cf. *Cyphastrea* sp.		3								1		2					
Echinopora sp.	1									1							
Galaxea fascicularis		2															
Symphyllia sp.		1							1								
C HORIZON																	
Montipora sp.	5	4	1											3		3	4
cf. *Montipora* sp.	3	2												1	1		3
Pavona sp. cf. *gardneri*	1													1			
cf. *Pavona* sp.	1	1														1	1
Gardinoseris ponderosa		1															1
Pachyseris sp.	3			1*										4*			
Porites sp. gp. 2	2	6	4				1		6	1		1		1	4		
cf. *Porites* sp. gp. 2		1															1
Goniopora sp.		2											1				1
Favia sp. gp. 1	16	12							2		2		14		2	3	5
Goniastrea pectinata	8	4	1	1						1			4	1	1	1	6
G. sp.	2	1								1			1			1	
cf. *Goniastrea* sp.	2													1		1	
Platygyra lamellina			1														1
P. sp.	1	1		1					2							1	
cf. *Leptoria* sp.		1													1		
Hydnophora sp.	3													2			1
Leptastrea sp. gp. 1	1	1	1										1	1			1
L. sp.	1												1				
Cyphastrea micropthalma	4													1		2	1
C. sp.	19	5											9	3	3	3	6
cf. *Cyphastrea* sp.	2												1				1
Echinopora gemmacea	3													2	1		
E. sp.	2	4												2	3		1
Galaxea fascicularis		1															
Merulina sp.	6												1	4			1
Lobophyllia sp.	1																
Symphyllia sp.		1							1								
cf. *Physophyllia* sp.	1												1				

from medium to large massive corals in the B horizon to small encrusting corals in the C. Such a trend is, of course, largely to be expected, for any patch with a C horizon of substantially greater volume than the B would be inherently unstable. Nevertheless, the scale of the size reduction between these two horizons is considerable, and would seem to be largely due to the comparative rarity of later-colonizing massive corals. This lack of massive C horizon corals can be partly explained by the fact that the encrusting species (such as *Cyphastrea* and *Montipora*), by virtue of their faster substrate-covering rates, would have pre-empted many of the available surfaces for colonization: however, there are still, throughout the area, many large B horizon corals which could have been colonized by massive C horizon colonies, but were not. It would seem, in fact, that the massive species present in this area (especially *Porites* sp. gp. 2) showed a marked preference for colonizing soft substrates.

Porites sp. gp. 2 is easily the most important B horizon coral at these four sites: 55% (by number) and 83% (by importance value) of all the B horizon corals belong to this species group (text-fig. 8 and Table 2). In terms of colony size, massive *Porites* is also the most important contributor to the C horizon (text-fig. 8), but this is only by virtue of the presence of a small number of very large colonies. Whereas *Porites* sp. gp. 2 comprises 47% of the C horizon by importance value, it comprises only 10% by number of colonies. Numerically more important forms in the C horizon are *Montipora* (*M.* sp. and cf. *M.* sp.), *Favia* sp. gp. 1, *Goniastrea* (principally *G. pectinata* and *G. retiformis*), and *Cyphastrea* (*C. micropthalma* (Lamarck) and *C.* sp.) (text-fig. 8). There are also a number of very small colonies of *Echinopora* (*E. gemmacea* (Lamarck) and *E.* sp.), *Merulina* sp., and *Pachyseris* sp. (Table 2).



TEXT-FIG. 8. Principal coral types in the B and C horizons at Sites 21–24. The left-hand portion of each bar in the histograms denotes percentage importance in terms of total number of colonies (N) and the right-hand portion percentage importance in terms of total importance values (IV). Coral groupings: *Montipora* (= *M.* sp. + cf. *M.* sp.); *Favia* (= *F.* sp. gp. 1); *Goniastrea* (= *G. retiformis* + *G. pectinata*); *Cyphastrea* (= *C. micropthalma* + *C.* sp.); *Echinopora* (= *E. gemmacea* + *E.* sp.).

The Nyali Quarry

Approximately 7–8 m of reef limestone is exposed above a lower quartz sands unit in the Nyali Quarry (Site 26) (text-figs. 2 and 4). The reef in this area is predominantly composed of isolated doming-massive coral colonies and small patches (within the size range 0·5 × 0·5 m to 4 × 4 m) set in a *Halimeda*-rich calcarenite. At first sight, the distribution of these corals and patches appears to be random, but closer inspection of the main north and east faces reveals a well-defined level (approximately half-way up each face) where a number of coral colonies and patches begin. There is no immediate evidence to suggest that this surface is subaerial in origin, and the lithologies above and below it are essentially similar. It is much less obvious along the southern edge of the quarry (if indeed it is present there at all), and probably represents a local pause in reef development rather than a complete stratigraphical break. It is believed that the reef deposits exposed in the Nyali Quarry are part of the main reef limestones of the Kenya coast and laterally equivalent to those exposed in the Nyali Creek (Crame 1977).

Detailed investigations of the patch faunas were made in the south-western embayment of the quarry (text-fig. 4). Here, there is no evidence of the discontinuity seen in the north and east faces, and patches are developed at various levels through the face. Nine patches (A–I), occurring in a rectangular plot measuring 32·0 × 2·5 m, were mapped in detail: the size of the study plot at each patch and the respective heights of the plots above the basal sands layer are given in Table 3. With the exception of patch E (which has only one B horizon coral), each of these patches is a composite structure containing more than one generation of B horizon corals, varying amounts of *Halimeda* calcarenite and encrusting algae, and several generations of C horizon corals.

TABLE 3. Patches studied in the south-western embayment of Nyali Quarry

Patch	Study plot size	Height of base of plot above sands
A	3·5 × 2·5 m	On sands
B	0·75 × 0·5 m	0·5 m
C	1·5 × 2·0 m	On sands
D	0·75 × 1·0 m	0·3 m
E	1·3 × 1·0 m	1·0 m
F	2·5 × 1·5 m	0·4 m
G	1·4 × 0·8 m	1·4 m
H	2·0 × 1·0 m	0·5 m
I	2·5 × 1·5 m	On sands

The earliest indications of reef growth in the south-western embayment of Nyali Quarry are in fact found in the topmost layer of the lower sands formation (text-fig. 4). Here, an abundant fauna, in which small coral colonies and molluscs predominate, indicates that reef development initiated in very shallow water conditions (Crame 1977, p. 199). However, this early fauna was soon replaced by one in which a number of large, isolated patches developed, and this change can be taken to reflect a fairly abrupt increase in water depth in this area (Crame 1977, p. 214). The *Halimeda* calcarenite which accumulated between these later coral patches supported a moderately diverse mollusc-echinoid fauna.

The greater density of patches in this area, presence of *Halimeda*, molluscs, and echinoids, and absence of extensive rubble deposits, all indicate that there were more equable conditions for reef growth here than at Sites 21–24. The patches at this site also developed to the lee of the large bank of stagshorn *Acropora* at Site 16 (text-fig. 4), but there were never any extensive influxes of reef rubble. It is likely that shallower water conditions prevailed here than at Sites 21–24 (Crame 1977, p. 214), but there is no evidence to suggest that any of the patches investigated built up to wave base.

Ecological stratification at Study plots A–I. Patch A developed in three clearly defined stages (text-fig. 9).

There is an initial fauna of small B horizon *Porites* colonies that grew almost directly on the lower sands formation, followed by two successive stages dominated by a mixture of large and small B horizon *Porites* (text-fig. 9). Despite the presence of these large B horizon corals, very few C horizon corals subsequently developed. There are in fact only four C horizon corals on patch A, and only one of these (a *Favia* sp. gp. 1) grew to an appreciable size (Table 4). A more extensive C horizon is present on patch C (text-fig. 10), which grew up from the top of the underlying sands formation. The core of the patch is formed by B horizon *Porites* colonies, and on the outer surfaces there are thick and thin encrusting colonies of *Montipora*, *Pavona*, and a variety of faviids (text-fig. 10 and Table 4). Patches B and D are small features centred on clumps of *Galaxea fascicularis* (Lamarck) and two small faviids, respectively. They each bear very limited C horizons (Table 4). Patch E is simple, containing only one B horizon coral (Table 4), but patch F is more complex, with a B horizon composed of thick-branching *Acropora*, massive *Porites*, and a single large colony of *Leptastrea* sp. gp. 2. C horizon corals on this low patch include encrusting colonies of *Montipora*, *Astreopora*, *Alveopora*, and *Acropora*, and the faviids *Goniastrea* and *Platygyra* (Table 4). Small faviids form the core of patch G and numerous spikey clumps of *G. fascicularis* the core of patch H. However, on both these patches there are only very limited C horizons. The three large B horizon *Porites* colonies in patch I support a C horizon containing a number of encrusting colonies of *Montipora* and several small domes of *Favia* sp. gp. 1 (Table 4).

TEXT-FIG. 9. Patch A, Site 26. *Key*: 1. *Porites* sp. gp. 2 (B horizon); 2. *Galaxea fascicularis* (C); 3. *Favia* sp. gp. 1 (C). Horizontal and vertical grid interval: 0·5 m.

TABLE 4. Principal B and C horizon corals at Site 26. N—number of colonies; Total IV—total importance values. * denotes approximate value.

PATCH A		
B horizon corals	*N*	*Total IV*
Stylophora cf. *pistillata*	1	0·50
Porites sp. gp. 2	11	722·00
	12	722·50
C horizon corals		
Pavona sp.	1	1·50
Favia sp. gp. 1	1	31.00
cf. *Favia* sp. gp. 1	1	1·00
Galaxea fascicularis	1	1·00
	4	34·50

PATCH B		
B horizon corals	*N*	*Total IV*
Galaxea fascicularis	6*	14·00
C horizon corals		
Montipora sp.	2	6·00
Favia sp. gp. 1	1	2·00
	3	8·00

PATCH C		
B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	4	170·00
Platygyra sp.	1	1·00
	5	171·00
C horizon corals		
Montipora sp.	1	1·50
cf. *Montipora* sp.	3	20·00
Pavona planulata	1	27·00
Porites sp. gp. 2	2	29·00
Favia sp. gp. 1	1	2·00
cf. *F.* sp. gp. 1	1	3·00
Goniastrea sp.	1	1·00
cf. *G.* sp.	2	3·00
Leptoria sp.	1	2·00
Echinopora sp.	3	3·00
Galaxea fascicularis	2	4·00
Acanthastrea sp.	1	3·00
	19	98·50

PATCH D		
B horizon corals	*N*	*Total IV*
Favia sp. gp. 1	1	7·00
Platygyra sp.	1	2·00
	2	9·00
C horizon corals		
Montipora sp.	1	5·00
Platygyra sp.	1	5·00
Echinopora sp.	1	2·00
	3	12·00

PATCH E		
B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	1	34·00
C horizon corals		
Montipora sp.	1	1·50
cf. *Montipora* sp.	1	2·00
Coscinarea sp.	1	0·50
Favia sp. gp. 1	1	1·50
Galaxea fascicularis	3	7·50
	7	13·00

PATCH F		
B horizon corals	*N*	*Total IV*
Acropora sp. gp. 9	2	4·00
Porites sp. gp. 2	1	15·00
Leptastrea sp. gp. 2	1	112·00
	4	131·00
C horizon corals		
Acropora sp. gp. 8	1	3·00
Astreopora sp.	2	5·00
Montipora sp.	4	32·50
cf. *Montipora* sp.	1	4·00
Alveopora sp.	1	0·50
Porites sp. gp. 2	1	3·00
Goniastrea pectinata	1	1·00
Platygyra sp.	1	23·00
Hydnophora sp.	1	0·25
Echinophyllia sp.	1	2·50
	14	74·75

PATCH G		
B horizon corals	*N*	*Total IV*
Favia sp. gp. 1	1	6·00
Cf. *F.* sp. gp. 1	1	5·00
Platygyra sp.	1	13·00
	3	24·00
C horizon corals		
Montipora sp.	1	12·00
cf. *Echinopora* sp.	1	4·00
	2	16·00

PATCH H		
B horizon corals	*N*	*Total IV*
Acropora sp. gp. 3	1	2·00
Montipora sp.	1	38·00
Galaxea fascicularis	25*	71·00*
	27*	111·00*
C horizon corals		
cf. *Montipora* sp.	1	3·00

PATCH I		
B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	3	374·00
C horizon corals		
Astreopora horizontalis	1	2·00
Montipora sp.	6	14·50
cf. *Montipora* sp.	4	13·00
cf. *Plesiastrea* sp.	1	1·50
Favia sp. gp. 1	4	9·50
Echinopora sp.	1	1·00
Galaxea fascicularis	1	0·75
cf. *Acanthastrea* sp.	1	1·00
	19	43·25

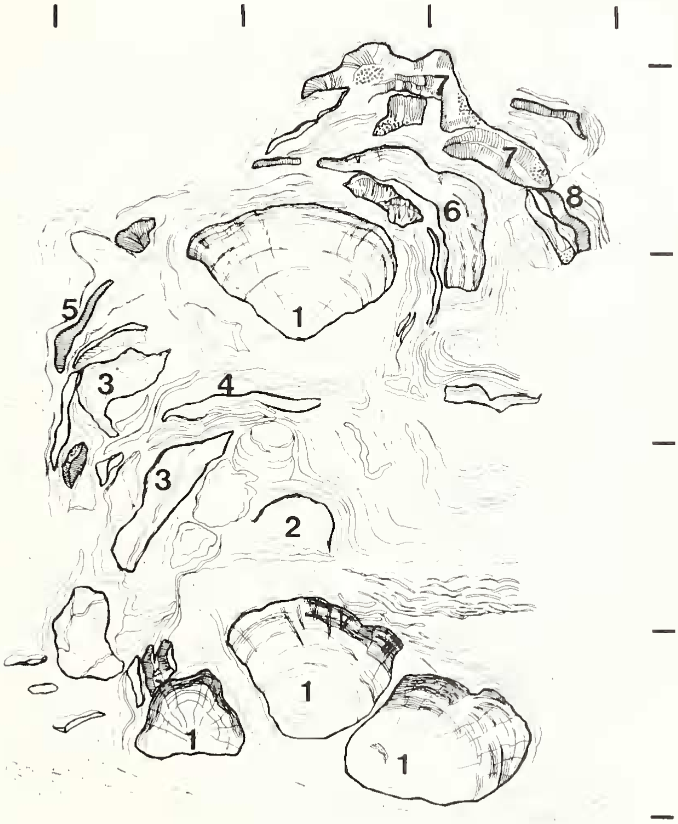
Combining the results from these nine patches shows that there is again a clear trend from medium to large, massive B horizon corals to small, encrusting C horizon corals (Table 5). Were it not for the presence of numerous spikey clumps of *G. fascicularis*, nearly all the B horizon corals would fall into the doming-massive growth form category, and but for the presence of a few colonies of *Favia* and *Galaxea*, the vast majority of C horizon corals would fall within growth form categories 6–9 (i.e. the encrusting types). Whereas the B horizon is spread through each of the importance value categories, the C horizon is concentrated in the two lowest categories (Table 5).

Porites sp. gp. 2 is again the most important B horizon coral (Table 5 and text-fig. 11). It comprises 83% of the B horizon (by importance value, text-fig. 11) and clearly played a fundamental role in patch formation. The only other prominent B horizon coral is *G. fascicularis*. It forms 48% (by number) of the B horizon (text-fig. 11), principally because of its abundance at patch H (Table 4). The foundations of this patch were formed by an interlayering of small, spikey *G. fascicularis* colonies and calcarenite matrix: each *Galaxea* colony appears to be based on calcarenite (i.e. B horizon) but in some instances it is extremely difficult to tell where one colony ends and another begins. There is a possibility that some of the colonies may have grown directly on top of others, but in general *G. fascicularis* adopts a B rather than a C horizon strategy (see Crame 1980, p. 9). Of the seven faviids in the B horizon, only one (a *Platygyra*) reached medium size, and one (a *Leptastrea* sp. gp. 2) very large size

(Table 5). The most important C horizon corals are thick platy- and doming-encrusting colonies of *Montipora* (= *M*. sp. and cf. *M*. sp.) (Table 5 and text-fig. 11). *Montipora* occupies 36% (by number) and 39% (by importance value) of the C horizon. Massive *Favia* (= *F*. sp. gp. 1 and cf. *F*. sp. gp. 1) is the next most important C horizon coral type, followed by encrusting colonies of *Porites* sp. gp. 2, *Goniastrea*, *Platygyra*, and *Echinopora* (text-fig. 11). There are also a few *G. fascicularis* colonies, and two small domes of *Astreopora* (Table 5; text-fig. 11).

The Diani and Msambweni Quarries

A series of small mounds and rises exposed in the cliff-line between Diani and Shimoni (text-fig. 2) reflect original reef topography. They are believed to be predominantly composed of shallow-water coral-algal assemblages and probably represent part of what was the outer margin of the Pleistocene reef (Crame 1977, p. 303; 1980, text-fig. 2). In the Diani–Msambweni–Shimoni region (text-fig. 12) these shallow-water mounds pass laterally (westwards) into a broad, back-reef region in which isolated coral colonies and small composite patches sporadically developed. All the exposures in this region are believed to be broadly contemporaneous and part of the main reef limestones of the Kenya coast (Crame 1977).



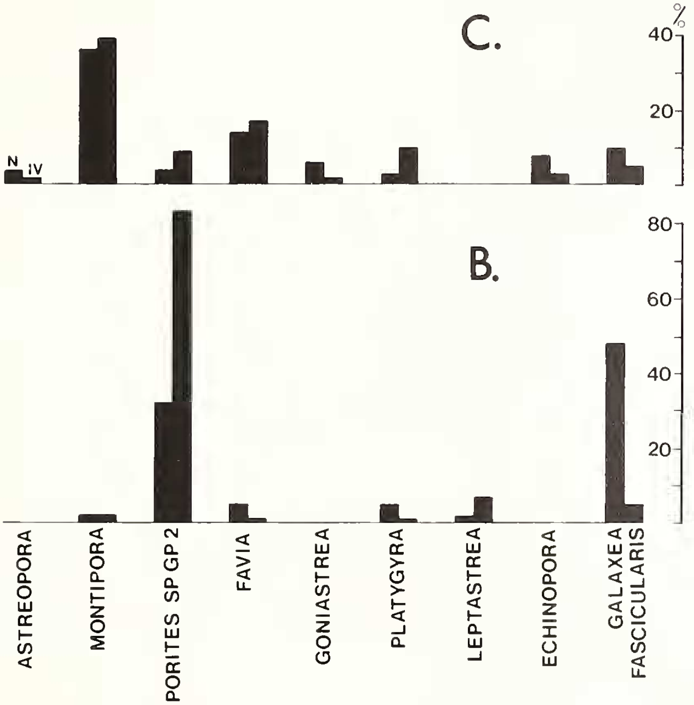
TEXT-FIG. 10. Patch C, Site 26. *Key*: 1. *Porites* sp. gp. 2 (B horizon); 2. *Platygyra* sp. (B); 3. cf. *Montipora* sp. (C); 4. *Montipora* sp. (C); 5. *Goniastrea* sp. (C); 6. *Porites* sp. gp. 2 (C); 7. *Pavona* sp. (C); 8. *Acanthastrea* sp. (C). Horizontal and vertical grid, 0·5 m.

TABLE 5. Summary of ecological stratification at Site 26. The table shows the number of B and C horizon occurrences of each coral species within the various importance value and growth-form categories. Groupings of these categories as for Table 2. N.B. The growth forms of *Stylophora* sp. cf. *pistillata* (Esper), *Acropora* sp. gp. 3, *A.* sp. gp. 9, and *Galaxea fascicularis* fall outside the growth-form scheme. * denotes approximate value.

	IMPORTANCE VALUES							GROWTH FORMS								
	0–1	2–10	11–20	21–50	51–100	101–200	201–300	1 Dom.-mass.	2 Dom.-encr. lyrs.	3 Mass.-irreg.	4 Mass.-tub. & pill.	5 Tiny domes & pat.	6 Platy-encr. thin	7 Platy-encr. thick	8 Dom.-encr. thin	9 Dom.-encr. thick
B HORIZON																
Stylophora sp. cf. *pistillata*	1															
Acropora sp. gp. 3		1														
A. sp. gp. 9		2														
Montipora sp.				1										1		
Porites sp. gp. 2		5	3	3	4	4	1	20								
Favia sp. gp. 1		2						2								
cf. *Favia* sp. gp. 1		1						1								
Platygyra sp.	1	1	1					3								
Leptastrea sp. gp. 3						1		1								
Galaxea fascicularis	15*	15*														
C HORIZON																
Acropora sp. gp. 8		1								1						
Astreopora horizontalis		1						1								
A. sp.		2						1						1		
Montipora sp.	3	11	1	1									1	6	3	6
cf. *Montipora* sp.	2	7	1										2	5		3
Pavona planulata				1												1
P. sp.	1												1			
Coscinarea sp.	1												1			
Alveopora sp.	1												1			
Porites sp. gp. 2		2		1										2		1
cf. *Plesiastrea* sp.	1												1			
Favia sp. gp. 1	3	4		1				7				1				
cf. *Favia* sp. gp. 1	1	1						1					1			
Goniastrea pectinata	1												1			
G. sp.	1											1				
cf. *Goniastrea* sp.	1	1											1	1		
Platygyra sp.		1		1												2
Leptoria sp.		1							1							
Hydnophora sp.	1											1				
Echinopora sp.	4	1											3	2		
cf. *Echinapora* sp.		1												1		
Galaxea fascicularis	3	4														
Acanthastrea sp.		1												1		
cf. *Acanthastrea* sp.	1													1		
Echinophyllia sp.		1											1			

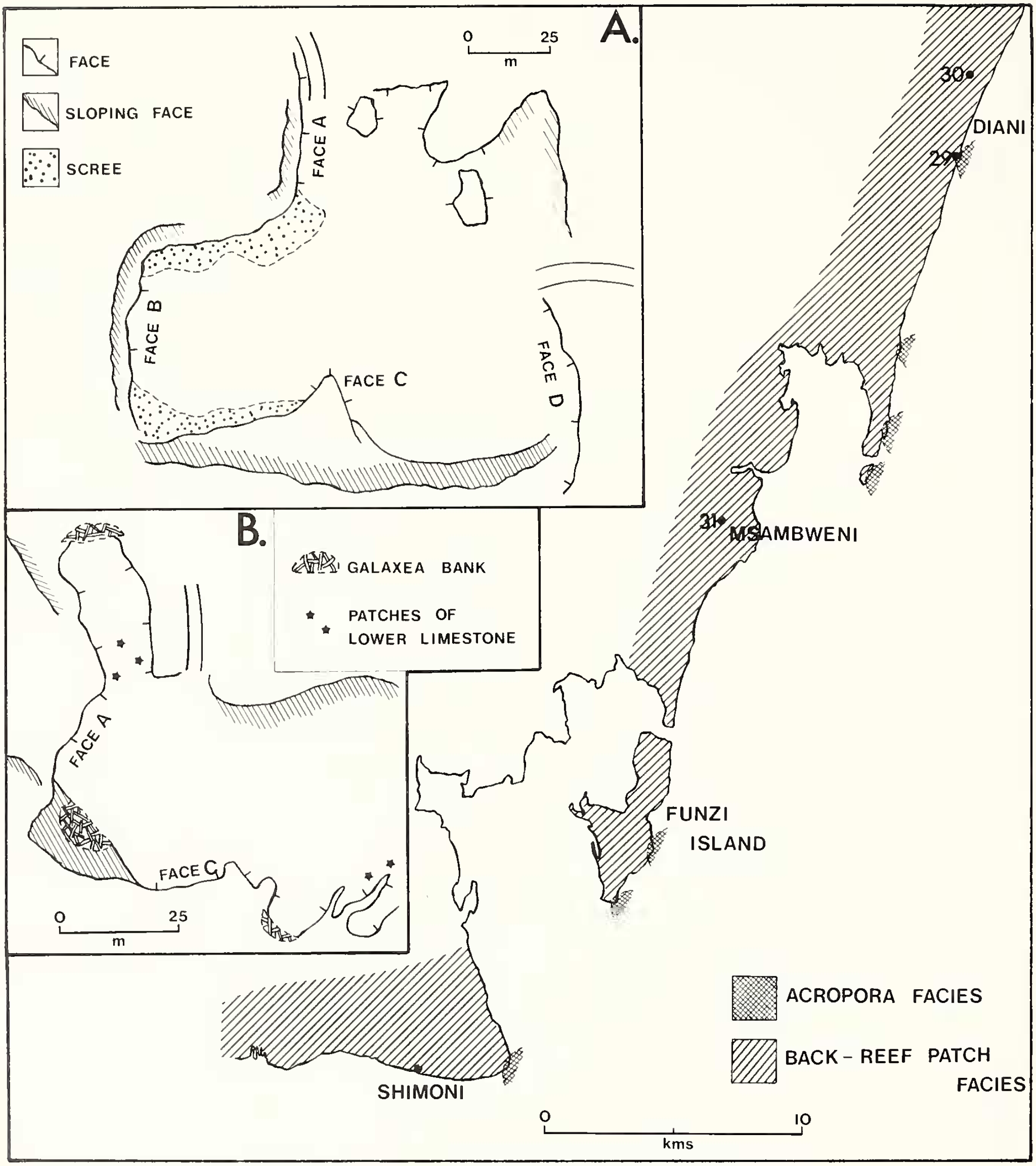
The transition from the outer shallow-water reef knolls to the inner back-reef facies is well seen in the Diani region (text-fig. 12). At Site 29 a small knoll measuring approximately 20 m (maximum width) by 3 m (height in the centre) is composed of a thick framework of encrusting calcareous algae and shallow-water corals (including a variety of small branching *Acropora* colonies and several massive-encrusting colonies of *Favia stelligera* (Dana). This knoll is believed to have developed in extremely shallow water and at times the top of it may have been exposed above wave base (Crame 1977, p. 254). Passing directly inland from Site 29 there is an abrupt change into a rather barren calcarenite facies that contains only scattered coral colonies and small composite patches. This facies is best exposed in Diani Quarry (Site 30, text-fig. 12), where the sporadic occurrence of corals forms a marked contrast to the thick frame assemblage at Site 29. Whereas 30% of the mound at Site 29 is composed of frame coral and algal material, the equivalent figure for the four sub-sites studied at Site 30 is only 3%.

This is not to say that there was necessarily a sharp depth gradient between Sites 29 and 30, for there is evidence to suggest that the latter developed in shallow water of no more than a few metres depth. The presence of a number of colonies of *Acropora* sp. gp. 3, *Montipora*, and encrusting *Pavona* suggests shallow, open-water conditions, as does a diverse molluscan assemblage containing strombid and trochid gastropods, and bivalves such as *Gloripallium*, *Spondylus*, *Anadara*, *Trachycardium*, *Timoclea*, and *Pitar*. In fact this molluscan assemblage is remarkably similar to that which developed on the *Halimeda* substrate between the coral patches in Nyali Quarry (Site 26) (Crame 1977, pp. 381–382). This resemblance no doubt reflects the similar positions occupied by the two sites on the Pleistocene reef. Site 26, like Site 30, was situated only a short distance behind a shallow-water outer reef assemblage, and it is thought that the water depth in both regions was broadly comparable (i.e. probably in the 1–10 m range). Present-day molluscan assemblages in which strombid and trochid gastropods, together with bivalves such as *Anadara*, *Trachycardium*, and *Pitar*, flourish are common on shallow, subtidal sand flats bearing scattered coral heads (e.g. Macnae and Kalk 1962; Maxwell 1968; Kay and Switzer 1974; Gibbs 1975, 1978).



TEXT-FIG. 11. Principal coral types in the B and C horizons at Site 26. The left-hand portion of each bar in the histograms denotes percentage importance in terms of total number of colonies (N) and the right-hand portion percentage importance in terms of total importance values (IV). Coral groupings: *Astreopora* (= *A. horizontalis* de Blainville + A. sp.); *Montipora* (= *M.* sp. + cf. *M.* sp.); *Favia* (= *F.* sp. gp. 1 + cf. *F.* sp. gp. 1); *Goniastrea* (= *G. pectinata* + *G.* sp. + cf. *G.* sp.); *Platygyra* (= *P.* sp.); *Leptastrea* (= *L.* sp. gp. 2); *Echinopora* (= *E.* sp. + cf. *E.* sp.).

The reef deposits exposed in the region of Msambweni Quarry (Site 31, text-fig. 12) differ in a number of ways from those exposed in Diani Quarry. Firstly, they are somewhat thinner (having a maximum thickness of 3 m compared to the 4·5 m in Diani Quarry), and secondly, they rest on a distinct lower limestone unit (Crame 1977, pp. 13 and 282). Isolated coral colonies and small patches are again exposed (set in a calcarenite matrix), but there are also a number of large banks of *Galaxea*



TEXT-FIG. 12. A facies and locality map for the Diani–Msambweni–Shimoni region. Inset A is a plan of Diani Quarry (Site 30) showing the four faces (A–D) studied. Inset B is a similar plan of Msambweni Quarry (Site 31) showing the positions of Faces A and C.

clavus (Dana) in this area (text-fig. 12). The three banks exposed in Msambweni Quarry (text-fig. 12) have maximum linear dimensions of 8, 12, and 8 m respectively, and maximum thicknesses of approximately 1·0–1·5 m. Finally, there is a rich, bivalve-dominated molluscan assemblage in this region which indicates even shallower-water conditions than at Site 30 (Crame 1977, p. 382).

Reef growth began in the Msambweni area with very shallow-water conditions, for there is evidence that the vertical development of several massive corals which grew directly on the lower limestone unit was tidally controlled (Crame 1977, p. 282). At a later stage the water depth evidently increased, for a number of large, uninterrupted doming-massive corals subsequently developed. However, this depth increase could only have been moderate, as the molluscan assemblage is a shallow-water one, and there is evidence to suggest that some of the largest *G. clavus* banks may have built up close to wave base. In particular, a C horizon coral assemblage present on the upper surface of a *G. clavus* bank at Site 31A (text-fig. 12) suggests that intertidal conditions may have subsequently been reimposed (Crame 1977, p. 295).

TABLE 6. Principal B and C horizon corals at Sites 30 and 31. N—number of colonies; Total IV—total importance values. * denotes estimated value.

SITE 30

FACE A

B horizon corals	*N*	*Total IV*
Acropora sp. gp. 3	2	14·00
Montipora sp.	2	16·00
Favia sp. gp. 1	1	2·00
cf. *Goniastrea* sp.	1	4·00
Platygyra sp.	2	17·00
cf. *Leptastrea* sp. gp. 2	1	5·00
Galaxea fascicularis	1	6·00
Lobophyllia sp.	2	95·00
Symphyllia sp.	1	13·00
	13	172·00
C horizon corals		
Porites sp. gp. 2	1	0·50

FACE B

B horizon corals	*N*	*Total IV*
Acropora sp. gp. 3	2	45·00
Porites sp. gp. 2	2	90·00
Goniopora sp.	1	4·00
Plesiastrea versipora	1	9·00
cf. *Plesiastrea* sp.	2	8·50
Favia sp. gp. 1	2	13·00
Goniastrea sp.	4	15·00
cf. *G.* sp.	2	25·50
Platygyra lamellina	1	7·00
P. sp.	3	14·00
Hydnophora exesa	1	5·00
Echinopora sp.	3	161·00
Galaxea clavas	1	82·00
Lobophyllia sp.	3	43·00
	28	522·00
C horizon corals		
Montipora sp.	1	2·00
Echinopora gemmacea	1	6·00
	2	8·00

FACE C

B horizon corals	*N*	*Total IV*
Acropora sp. gp. 3	2	11·00
Montipora sp.	1	0·75
Porites sp. gp. 2	4	35·00
Goniastrea sp.	1	4·00
cf. *G.* sp.	1	18·00
Echinopora sp.	1	2·00
Galaxea fascicularis	5	38·00
Lobophyllia corymbosa	2	82·00
Symphyllia sp.	1	0·50
	18	191·25
C horizon corals		
Acropora sp. gp. 3	1	4·00
Montipora sp.	1	1·00
Pavona sp.	2	19·00
cf. *P.* sp.	11	112·00
Favia sp. gp. 1	3	4·00
cf. *Goniastrea* sp.	1	0·50
Galaxea fascicularis	1	2·00
Acanthastrea echinata	2	1·50
	22	144·00

FACE D

B horizon corals	*N*	*Total IV*
Montipora sp.	2	3·75
Porites sp. gp. 2	2	128·00
Favia sp. gp. 1	1	6·00
Platygyra sp.	1	21·00
cf. *Goniastrea* sp.	1	3·00
Hydnophora sp.	1	3·00
Echinopora sp.	7	40·00
cf. *Acanthastrea* sp.	1	3·00
Lobophyllia cf. *hemprichii*	1	3·00
L. sp.	2	123·00
Symphyllia sp.	1	4·00
	20	337·75
C horizon corals		
cf. *Montipora* sp.	2	40·00
Favia sp. gp. 1	1	0·75
Favites sp.	1	6·00
Cyphastrea sp.	1	21·00
Echinopora sp.	1	9·00
Galaxea fascicularis	1	1·00
	7	77·75

SITE 31

FACE A

B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	1	75·00
Favia sp. gp. 1	2	14·00
cf. *Favia stelligera*	1	2·00
Favites sp.	1	46·00
cf. *Goniastrea* sp.	1	5·00
Platygyra sp.	2	59·00
Leptastrea sp. gp. 2	1	72·00
Echinopora gemmacea	1	6·00
Physogyra sp.	3	31·00
	13	310·00
C horizon corals		
Montipora sp.	1	2·00
Favia sp. gp. 1	1	6·00
	2	8·00

FACE C

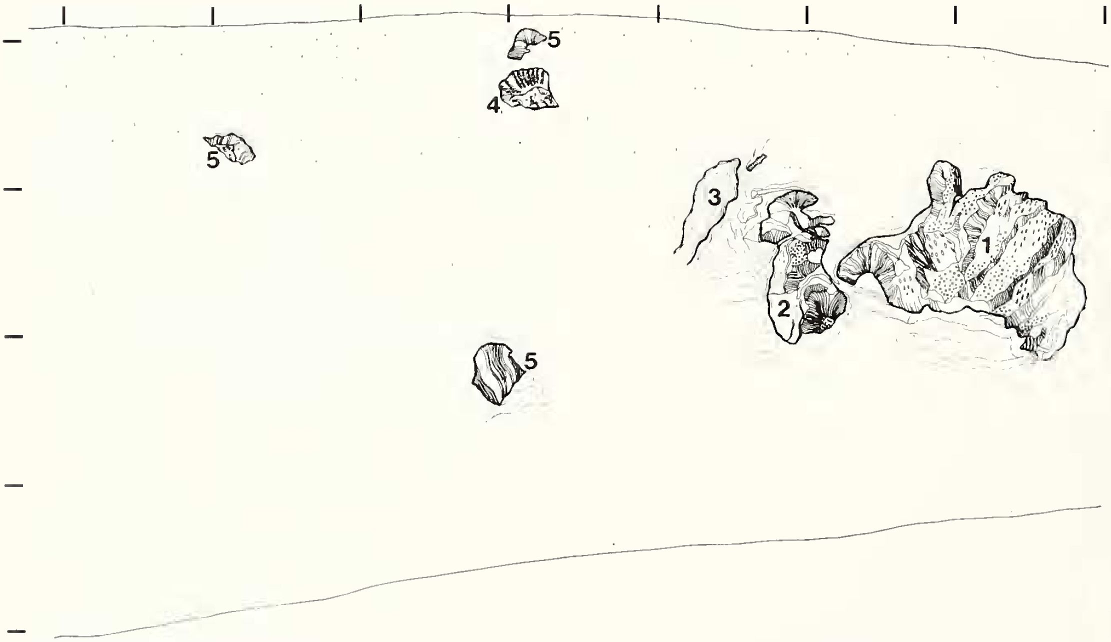
B horizon corals	*N*	*Total IV*
Porites sp. gp. 2	2	185·00
Favia sp. gp. 1	1	31·00
Goniastrea incrastans	1	29·00
G. sp.	4	64·00
cf. *G.* sp.	1	4·00
Platygyra lamellina	1	52·00
P. sp.	3	82·00
Leptastrea sp.	1	11·00
Hydnophora sp.	1	29·00
Galaxea clavas	1	60·00*
Lobophyllia corymbosa	1	31·00
L. sp.	1	9·00
	18	587·00*
C horizon corals		
Montipora sp.	2	4·00
cf. *Montipora* sp.	1	0·75
cf. *Goniopora* sp.	1	3·00
	4	7·75

Stratification in the Diani Quarry (Site 30). Four sub-sites were studied in the Diani Quarry (Faces A, B, C, and D; text-fig. 12).

Face A (approximate size of study plot: 18 × 3 m). This face contains a very sparse assemblage of isolated coral colonies set in a *Halimeda*-rich calcarenite. The corals are typically small to medium in size, and all but one belongs to the B horizon. Indeed, it is a noticeable feature of both Diani and Msambweni Quarries that the B horizon is considerably more diverse than the C (Table 6). In addition to massive colonies of *Lobophyllia*, *Symphyllia*, and several types of faviid, there are also two encrusting colonies of *Montipora* and two corymbose colonies of branching *Acropora* in the B horizon (Table 6). The C horizon contains only one small colony of *Porites* sp. gp. 2.

Face B (30 × 3 m) (text-fig. 13). The coral assemblage in this face is very similar to that exposed in Face A. Again, there is a variety of B horizon types (Table 6), but these are all widely separated and there are no conspicuous aggregations of corals (text-fig. 13). There are medium-sized colonies of *Porites* sp. gp. 2, *Lobophyllia*, and *Acropora* sp. gp. 3, a variety of small doming and encrusting faviids, and one very large, thick-encrusting *Echinopora* (text-fig. 13). There is also a large colony of *G. clavus* in the B horizon, but the C horizon is again very restricted (Table 6).

Face C (studied in two sections: combined plot size—18·0 × 2·5 m). Although corals are still sparsely distributed in this face, there is some evidence of more intensive stratification. There are three small composite patches, and one large one which seems to be predominantly composed of a sequence of C horizon colonies of encrusting *Pavona*. However, it should be pointed out that the assignment of eleven colonies of cf. *Pavona* sp. in this patch to the C horizon (Table 6) is somewhat tentative. Large, encrusting colonies of *Pavona* are notoriously complex, and it is just possible that these eleven domes could in fact be part of a single, complex B horizon coral (Crame 1977, p. 273). Nevertheless, there are also encrusting colonies of *Montipora* sp., *Pavona* sp., and *Acanthastrea echinata* (Dana) in the C horizon, together with small clumps of *Acropora* sp. gp. 3 and *Galaxea fascicularis*, and tiny domes of *Favia* and cf. *Goniastrea* sp. A noticeable addition to the B horizon in this face is a number of colonies of *G. fascicularis* (Table 6).



TEXT-FIG. 13. Part of Face B, Site 30. *Key*: 1. *Echinopora* sp. (B horizon); 2. cf. *Goniastrea* sp. (B); 3. *Porites* sp. gp. 2 (C); 4. *Lobophyllia* sp. (B); 5. *Platygyra* sp. (B). Horizontal and vertical grid interval: 0·5 m.

Face D (21·0 × 2·5 m) (text-fig. 14). Prominent in the B horizon in this face are small colonies of platy-encrusting *Echinopora*, and several medium to large-sized domes of *Porites* sp. gp. 2 and *Lobophyllia* (Table 6). Other types present include *Montipora* sp., cf. *Acanthastrea* sp., *Symphyllia* sp., and a variety of small faviids, but as in the other three faces these corals are all widely spaced. Two small composite patches are present (text-fig. 14), and these provide bases for C horizon encrusting colonies of cf. *Montipora* sp., *Cyphastrea*, and *Echinopora* (Table 6).

TEXT-FIG. 14. Part of Face D, Site 30. *Key*: 1. *Montipora* sp. (B horizon); 2. *Pavona* sp. (C); 3. core of *Acropora* sp. gp. 3 and *Galaxea fascicularis*; 4. *Cyphastrea* sp. (C); 5. *Favia* sp. gp. 1 (C); 6. *Favites* sp. (C); 7. cf. *Montipora* sp. (C); 8. *Echinopora* sp. (C). Horizontal and vertical grid, 0·5 m.

Stratification in the Msambweni Quarry (Site 31). Two sites (Faces A and C, text-fig. 12) were studied in this quarry to investigate the patch fauna which developed between the large *G. clavus* banks. The base of the study plots on both these faces lies approximately 0·5 m above the top of the lower limestone unit.

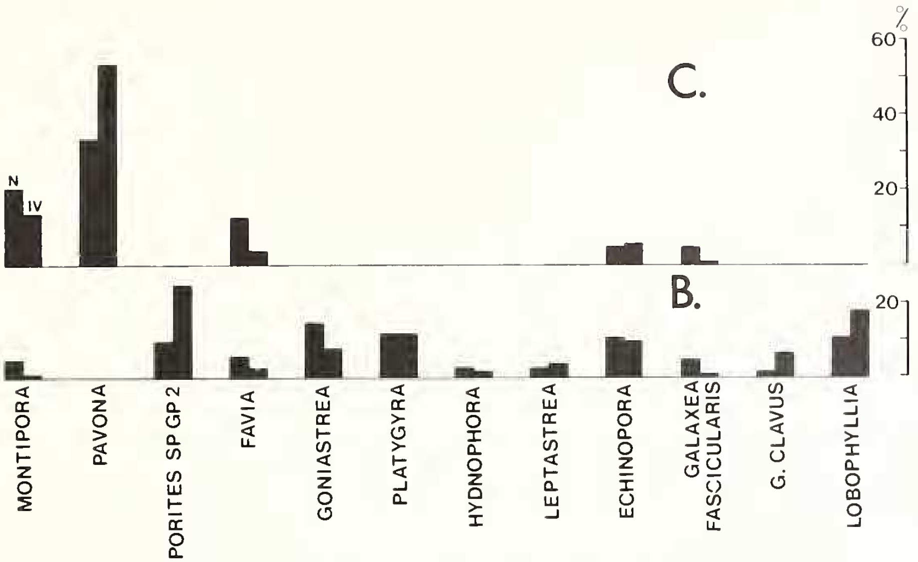
Faces A and C (study plot sizes—14·0 × 2·8 m and 38·0 × 2·8 m, respectively. The coral faunas exposed in these two faces are very similar in appearance to those examined in the Diani Quarry. Isolated doming-massive and encrusting colonies predominate, and again there has been comparatively little ecological stratification (Table 6). Medium to large faviids are particularly common in the B horizons, along with several large colonies of massive *Porites*, *Lobophyllia*, and *G. clavus*. A distinctive addition to the B horizon in Face A is the caryophyllid genus *Physogyra* (Table 6).

Summary of ecological stratification at Sites 30 and 31

When the results from the various faces at these two sites are combined (Table 7), it becomes apparent that similar stratification trends to those seen at Sites 21–24 and 26 can be detected (cf. Tables 2, 5, and 7). The B horizon again has a range of small to large colonies with predominantly massive growth forms, whilst the C horizon is mainly composed of small platy- and doming-encrusting colonies and tiny patches. However, this trend is slightly less obvious at these sites, principally because a number of B horizon corals occur in the later growth-form categories (i.e. categories 5–11, Table 7). In particular, there are a number of B horizon colonies of branching *Acropora* and encrusting types such as *Montipora*, *Hydnophora*, and *Echinopora*.

TABLE 7. Summary of ecological stratification at Sites 30 and 31. The table shows the number of B and C horizon occurrences of each coral species within the various importance value and growth-form categories. Grouping of these categories as for Table 2. N.B. The growth forms of *Acropora* sp. gp. 3, *Galaxea fascicularis*, *G. clavus*, and *Lobophyllia* fall outside the growth-form scheme.

	IMPORTANCE VALUES						GROWTH FORMS								
	0–1	2–10	11–20	21–50	51–100	101–200	1 Dom.-mass.	2 Dom.-encr. lyrs.	3 Mass.-irreg.	4 Mass.-tub. & pill.	5 Tiny domes & pat.	6 Platy-encr. thin	7 Platy-encr. thick	8 Dom.-encr. thin	9 Dom.-encr. thick
B HORIZON															
Acropora sp. gp. 3		5		1											
Montipora sp.	2	2	1									2		1	2
Porites sp. gp. 2		3	1	2	4	1	9		2						
Goniopora sp.		1					1								
Plesiastrea versipora		1							1						
cf. *Plesiastrea* sp.	1	1					1						1		
Favia sp. gp. 1		6		1			5	1							1
cf. *Favia stelligera*		1											1		
Goniastrea incrustans				1				1							
G. sp.	1	5	2	1			2	4	1				1	1	
cf. *Goniastrea* sp.	1	4	1	1			2	1	4						
Favites sp.				1				1							
Platygyra lamellina		1			1		1	1							
P. sp.	1	4	2	4			4	4	2						1
Hydnophora exesa		1											1		
H. sp.		1		1				1					1		
Leptastrea sp. gp. 2					1		1								
cf. *Leptastrea* sp. gp. 2		1					1								
L. sp.			1					1							
Echinopora gemmacea		1											1		
E. sp.	1	7	1	1		1		2				1	7		1
Galaxea fascicularis	2	3	1												
G. clavus					2										
cf. *Acanthastrea* sp.		1											1		
Lobophyllia corymbosa			1	1	1										
L. sp. cf. *hemprichii*		1													
L. sp.		2	2	1	3										
Symphyllia sp.	1	1	1				2				1				
Physogyra sp.		1	2				3								
C HORIZON															
Acropora sp. gp. 3		1													
Montipora sp.	1	4												4	1
cf. *Montipora* sp.	1		1	1								1			2
Pavona sp.		2													2
cf. *Pavona* sp.	1	7	1	2											11
Porites sp. gp. 2	1										1				
cf. *Goniopora* sp.		1													1
Favia sp. gp. 1	3	2					1				3				1
Favites sp.		1					1								
cf. *Goniastrea* sp.	1										1				
Cyphastrea sp.				1											1
Echinopora gemmacea		1													1
E. sp.		1											1		
Galaxea fascicularis	1	1													
Acanthastrea echinata	2											2			



TEXT-FIG. 15. Principal coral types in the B and C horizons at Sites 30 and 31. The left-hand portion of each bar in the histograms denotes percentage importance in terms of total number of colonies (N) and the right-hand portion percentage importance in terms of total importance values (IV). Coral groupings: *Montipora* (= *M.* sp.+cf. *M.* sp.); *Pavona* (= *P.* sp.+cf. *P.* sp.); *Favia* (= *F.* sp. gp. 1); *Goniastrea* (= *G. incrustans* Duncan + *G.* sp.+cf. *G.* sp.); *Platygyra* (= *P. lamellina* + *P.* sp.); *Hydnophora* (= *H. exesa* + *H.* sp.); *Leptastrea* (= *L.* sp. gp. 2+cf. *L.* sp. gp. 2 + *L.* sp.); *Echinopora* (= *E. gemmacea* + *E.* sp.); *Lobophyllia* (= *L. corymbosa* (Forskål) + *L.* sp. cf. *hemprichii* (Ehrenberg) + *L.* sp.

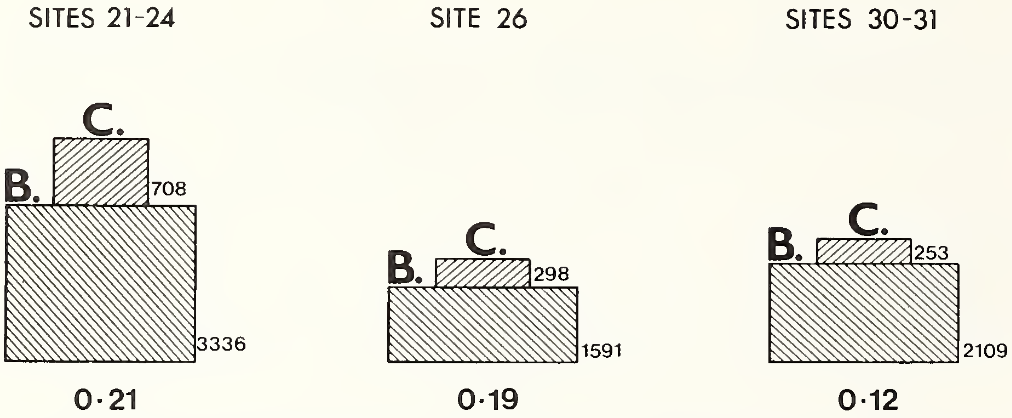
The most conspicuous B horizon coral is still *Porites* sp. gp. 2 (text-fig. 15). Nevertheless, its dominance over other coral types is not nearly so marked as at the other two sites investigated (cf. text-figs. 8, 11, and 15), and when numbers of colonies are considered, *Goniastrea*, *Platygyra*, *Echinopora*, and *Lobophyllia* are all found to be more prominent (text-fig. 15). Clearly, massive *Porites* was not able to dominate the B horizon to the same extent in the Diani–Msambweni area as it did in the Nyali area. The C horizon appears to be dominated by Pavona (= *P.* sp. and cf. *P.* sp.) (text-fig. 15), but it must be remembered that a number of colonies of cf. *Pavona* are only tentatively assigned to this horizon. Other important C horizon corals are *Montipora*, *Favia* sp. gp. 1 (of which there are again a large number of small colonies), and *Echinopora* (text-fig. 15).

DISCUSSION

The form of the Pleistocene reef

Preliminary investigations suggest that much of the widespread back-reef region of the Kenya Pleistocene reef was a comparatively shallow-water reef flat (Crame 1977, figs. 57, 79, and 80): in some parts of the region deeper water conditions permitted the establishment of large, *Acropora*-dominated banks, but elsewhere intertidal conditions prevailed (Crame 1977, 1980). There is no evidence that an extensive deep-water lagoon ever developed and it would seem that the closest Recent analogies would be some of the fringing reefs of the Australian Great Barrier Reef province (e.g. Maxwell 1968). Much of the back-reef facies of the Kenya Pleistocene reef resembles the quiet-water facies which developed on the central and north-western parts of the Aldabra platform during the last Interglacial (Braithwaite *et al.* 1973, fig. 21). The small size of so many of the patches also suggests that comparatively shallow-water conditions prevailed over much of the back-reef region.

Patch reefs are generally much bigger (and more densely grouped) in atoll than in shelf lagoons. In the former they frequently attain dimensions of tens, or even hundreds, of metres across and their vertical development is often such as to permit the establishment of a distinct zonation of their constituent coral faunas (e.g. Garrett *et al.* 1971; Bonem and Stanley 1977): Garrett, Smith, Wilson and Patriquin (1971, p. 664) have shown that in relatively shallow-water lagoons an approximate correlation exists between patch-reef size and water depth. Studies throughout the Indo-Pacific support this finding and indicate that broad, shallow-water reef flats typically support sparse assemblages of isolated coral heads and small, composite patches (e.g. Maxwell 1968; Rosen 1971, 1972; Stoddart 1973; Chevalier 1973; Morton 1974; Pillai 1977).



TEXT-FIG. 16. A comparison of the ratios of C to B horizon importance values in the three areas investigated. The figures by the side of each block are cumulative importance values and those beneath the three columns, the actual ratios.

Slightly deeper-water conditions existed in the region of Sites 19–24 than in either of the other two areas investigated. The presence of large individual colonies and patches (up to 4 m in height), extensive areas of very fine-grained sediment, and the presence of platy colonies of *Pachyseris* and *Merulina* (Crame 1977), all suggest a water depth in excess of 10 m, especially in the region of Site 24. There were certainly more open-water conditions at Site 26, and it is likely that the water depth here was only in the 1–10 m range: even shallower conditions probably existed in parts of the Diani–Msambweni–Shimoni region (Sites 30 and 31). These varying water depths appear to correlate with the amount of stratification observed in each of the three areas, for when the ratios of C to B horizon importance values are compared, it can be seen that there is a proportionately greater volume of C horizon corals at Sites 21–24 than at either Site 26 or Sites 30 and 31 (text-fig. 16). This larger C horizon may be partly a reflection of a greater density of very large B horizon corals at Sites 21–24, but it is probably also an indication of a genuine trend towards more extensive stratification in a deeper-water environment. A large number of B horizon corals were encountered at Sites 30 and 31, but only a very few of them supported any C horizon corals. On present-day reefs in the western Indian Ocean there is evidence that more extensive stratification occurs within *Porites* assemblages occupying deeper-water reef fronts and channels than in shallow-water platform assemblages (Rosen 1971, 1972; Barnes *et al.* 1971, and references cited above). However, a possible correlation between stratification and the prevalent sedimentary environment should also be considered, for it is known that in the deeper-water region of Sites 19–24 there were conditions of both increased fine sedimentation and periodic rubble incursions. It could be that such conditions rendered much of the substrate unsuitable for colonization by corals, so that many species had to settle and develop on existing structures rather than initiate new ones.

Principal B and C horizon corals

The single most important coral at Sites 21–24 is *Porites* sp. gp. 2. Large *Porites* colonies are present in both the B and C horizons, and the whole area has the appearance of a Recent quiet-water *Porites* assemblage (*sensu* Rosen 1971, 1972). In the western Indian Ocean such assemblages are characteristic of sheltered surface reef environments, and of water depths down to about 10 m or more in less sheltered surface environments. They are typically composed of species such as *P. lutea* Milne-Edwards and Haime and *P. solida* (Forskål), together with massive faviids such as *Favia favus* (Forskål), *F. pallida* (Dana), *Goniastrea retiformis*, *Favites halicora* (Ehrenberg), *Platygyra lamellina* (Ehrenberg), and *Leptoria phrygia* (Ellis and Solander) (Pichon 1964, 1971; Talbot 1965; Taylor 1968; Rosen 1971, 1972; Stoddart 1973). Large, isolated colonies of massive *Porites* are also common in the boat channel which is present along much of the East African reef platform (Talbot 1965; Crossland 1902, 1903). The predominance of *Porites* sp. gp. 2 in the B horizon at these sites can be readily linked to the known wide environmental tolerances of this group. Species of massive *Porites* are common in exposed habitats on reef flats (e.g. Manton 1935; Wells 1954; Mergner and Scheer 1974; Scoffin and Stoddart 1978), and are also known to be capable of withstanding conditions of reduced circulation and illumination, as well as considerable influxes of fine sediment (e.g. Mayor 1924; Marshall and Orr 1931; Manton 1935; Rosen 1972). Small colonies of *Porites* have been recorded as early colonizers on the Recent reef flats of Eilat (Red Sea) (Loya 1975, 1976) and in Oligocene patch reefs in the Caribbean (Frost 1977; Frost and Weiss 1979). Furthermore, in a recent study of the reefs of Enewetak Atoll, Highsmith (1980) has shown that not only is *P. lutea* a major structural component of lagoon patch and pinnacle reefs, but that it is also an important B horizon pioneer. It appears that massive colonies, or parts of them, periodically break off from the sides of existing patches, roll down on to the bare sands of the lagoon floor, and in turn initiate new reef structures. This may be a significant and hitherto unrecognized method of patch reef initiation.

No other tolerant corals are common in the B horizon at Sites 21–24. Massive faviids are rare, and there are only a few tolerant encrusting types, such as *Cyphastrea*. Faviids are, however, much more prominent in the C horizon. Here, there are a large number of small domes of *Favia* sp. gp. 1 and *Goniastrea*, as well as a smaller number of types such as *Platygyra* and *Leptastrea*. Tiny encrusting patches of *Cyphastrea* are particularly common in the C horizon, and there are also several colonies of platy *Echinopora*. All these types are known to be tolerant corals (e.g. Rosen 1972, and references therein), yet their occurrence at these four sites is essentially restricted to the C horizon. Other C horizon corals include *Porites* sp. gp. 2 (both massive and encrusting growth forms), encrusting *Montipora*, a few small pavonids (*Pavona*, *Gardineroseris*, and *Pachyseris*), and the oculinid, *Merulina*.

Porites sp. gp. 2 is also the most important B horizon coral at Site 26: there is one very large colony of *Leptastrea* sp. gp. 2, but massive faviids are again poorly represented. *Galaxea fascicularis* is a prominent B horizon coral in two of the patches, and this agrees well with its early colonizing role in areas of thick reef framework (Crame 1980). The biggest difference between Sites 21–24 and 26 lies in the nature of the encrusting corals in their respective C horizons. Whereas *Cyphastrea* is well represented at Sites 21–24, it is absent from Site 26. Here, encrusting *Montipora* is particularly common, and indeed is the single most important coral type in the C horizon. Encrusting *Montipora* is abundant on many recent shallow-water reef flats and edges (e.g. Manton 1935; Wells 1954; Newell 1956; Mergner and Scheer 1974), and its prominence at this site reflects the shallower-water conditions that are known to have existed in this area. Small domes of *Favia* sp. gp. 1 are common in the C horizon at Site 26, but the only other faviids are a few small encrusting colonies of *Goniastrea*, *Platygyra*, and *Leptoria*. *Acropora* sp. gp. 8, *G. fascicularis*, and small, encrusting colonies of *Astreopora*, *Coscinarea*, *Alveopora*, and *Acanthastrea* are all present at Site 26, but absent from Sites 21–24.

Analysis of the patch faunas at Sites 30 and 31 shows that whereas the B horizon is considerably more diverse than at any of the other sites investigated, the C horizon is relatively impoverished. Such a fauna, dominated by a variety of isolated B horizon corals, may well be a direct consequence of the shallow-water conditions that are known to have existed in this area. It is likely that the conditions of circulation, illumination, and oxygenation were slightly better in these shallow waters (compared with those at the other sites studied), and that a wider variety of pioneer coral types could become established. However, these same shallow waters must have placed constraints on the amount of vertical development that was possible on any one patch, and thus effectively limited the extent of stratification. The B horizon contains acroporids (*Acropora* sp. gp. 3 and *Montipora* sp.), *Porites* sp. gp. 2, and a range of massive faviids (with *Goniastrea* and *Platygyra* being the commonest types). There are also platy-encrusting colonies of *Hydnophora* and *Echinopora*, small, spikey clumps of *Galaxea fascicularis*, and several large mounds of *G. clavus*, *Lobophyllia*, *Symphyllia*, and *Physogyra* occur essentially as isolated B horizon hemispherical domes. The apparent prominence of *Pavona* (which includes cf. *P.* sp.) in the C horizon at Sites 30 and 31 is exaggerated by the aggregation of a number of colonies of cf. *P.* sp. on a single patch at Site 30. It is probably true to say that *Montipora* is more important, for it is certainly the most widespread C horizon coral. There are again a number of small domes of *Favia* sp. gp. 1, but no other coral types are at all common. A noticeable feature of the C horizon is that there is only one tiny colony of *Porites* sp. gp. 2.

It is possible to combine these results from the three areas studied to draw a number of general conclusions about the principal B and C horizon coral types in the Kenya Pleistocene reef. Table 8 lists the ten most important corals, as defined by their cumulative occurrences in either the B or C horizons. The first five corals (*Porites* sp. gp. 2, *Platygyra*, *Leptastrea*, *G. fascicularis*, and *Lobophyllia*) show, either by the total number of colonies or their total importance values, a marked preference for the B horizon, and the next three (*Montipora*, *Cyphastrea*, and *Favia*) a marked preference for the C. *Echinopora* and *Goniastrea* show approximately equal preference for either the B or C horizons.

It is readily apparent from Table 8 that *Porites* sp. gp. 2 is by far the most important B horizon coral in the Kenya Pleistocene reef. It occurs in all three of the areas investigated (being especially common at Sites 21–24 and 26), and its large, broad colonies often provided the only suitable substrates for subsequent colonization. Massive species of *Porites* were clearly of fundamental importance in patch-reef formation, as they are now throughout the Indo-Pacific province. Casual observations of early patch formation on both sandy reef flats and lagoon floors have suggested to a number of authors that massive *Porites* is one of the most important pioneer corals on soft substrates (e.g. Umbgrove 1947; Wells 1954; Talbot 1965; Wijsman-Best 1972; Stoddart 1973; Maragos 1974). This fundamental structural role in Indo-Pacific patch reefs is perhaps analogous to that played by the massive faviid *Montastrea annularis* (Ellis and Solander) in many Caribbean patch reefs (e.g. Goreau 1959; Milliman 1973). *Platygyra* is the most prominent B horizon faviid, but it must be emphasized that it is very much less important in patch reef formation than *Porites* sp. gp. 2 (Table 8). Another

TABLE 8. Principal B and C horizon corals in the Kenya Pleistocene reef. Total N—total number of colonies; Total IV—total importance values. *denotes approximate value.

	B HORIZON		C HORIZON	
	Total N	*Total IV*	*Total N*	*Total IV*
Porites sp. gp. 2	66	4608	16	361
Platygyra	17	277	6	92
Leptastrea	5	212	4	18
Galaxea fascicularis	36*	102	9	17
Lobophyllia	12	386	0	0
Montipora	9	71	49	203
Cyphastrea	8	75	31	58
Favia	14	117	43	117
Echinopora	13	210	17	49
Goniastrea	15	139	19	72

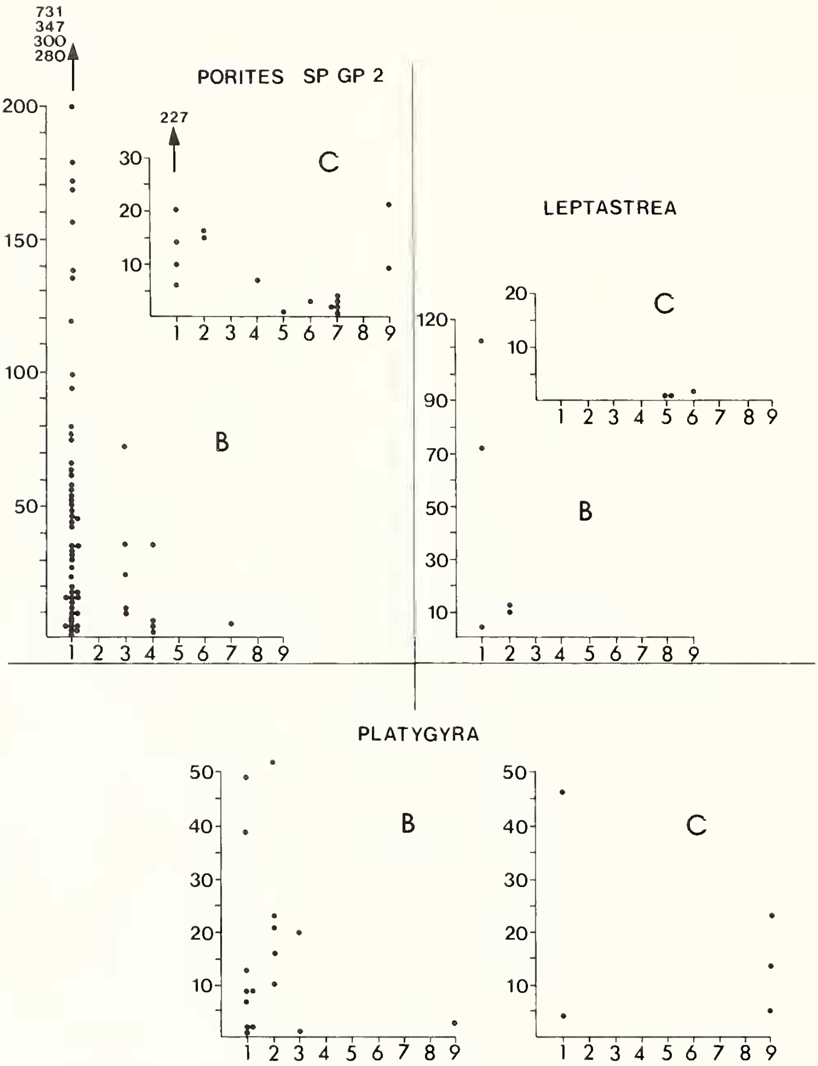
massive faviid, *Leptastrea*, also shows an apparent preference for occurrence as large colonies in the B horizon, but so far is known from only a very small number of specimens (Table 8). *Galaxea fascicularis*, in comparison with its occurrence in areas of thick reef framework (Crame 1980), is in fact a comparatively rare early colonizer in the back-reef region, and *Lobophyllia*, although entirely restricted to the B horizon, was never observed to bear any subsequent C horizon corals. The commonest C horizon corals in the Kenya Pleistocene reef are the encrusting forms *Montipora* and *Cyphastrea*, and massive *Favia* (Table 8).

A re-emphasis of the structural roles played by the principal coral types in patch reef formation

It is possible to illustrate the structural role played by each of the principal coral types by pooling data on substrate preferences, colony sizes, and growth forms from each of the sites investigated. If B horizon occurrences are first of all separated from C horizon ones, and then within these two categories the size (importance value) of each individual coral colony is plotted against its growth form, it should be possible to determine whether or not each of the principal corals adopted a consistent structural role in patch formation. For example, text-fig. 17 shows that colonies of *Porites* sp. gp. 2 are predominantly concentrated in growth-form category 1 (doming-massive) of the B horizon. *Porites* sp. gp. 2 has dominated this category to a far greater extent than any other coral type. It occurs over a very wide size range, and it is striking how few colonies fall within any of the other B horizon growth-form categories. The smaller number of C horizon occurrences of *Porites* sp. gp. 2 are more widely dispersed among the various categories (text-fig. 17): there are both doming and massive types (categories 1 and 2), as well as a number of very small encrusting colonies (categories 6–9). *Platygyra* also occurs over a variable size range within the low growth-form categories of the B horizon, and there is evidence to suggest that *Leptastrea* may too (text-fig. 17). Although there are as yet few data available for the latter coral type, both the large colonies recorded formed the cores to substantial patch structures.

Cyphastrea, a typical C horizon coral, plots predominantly in very small size classes within the last five growth form categories (i.e. 5–9, text-fig. 18). There are a few B horizon *Cyphastrea* colonies (domes formed out of successive encrusting layers and ‘tubular’ colonies), but by far the majority of colonies are very small C horizon patches and encrusting colonies. *Montipora*, another important C horizon coral, adopted very similar habits (text-fig. 18), and it would appear at first sight as if these two coral types may have played equivalent structural roles in patch reef formation. However, it has to be remembered that they do not co-occur extensively in the Kenya Pleistocene reef: *Cyphastrea* is typical of areas where there were conditions of reduced circulation and increased fine sedimentation (such as Sites 21–24) and *Montipora* of shallower, more open-water regions (such as Sites 26 and 30–31). A third common C horizon coral, *Favia* sp. gp. 1, typically occurs as small doming-massive colonies and tiny encrusting patches: very few colonies of *F.* sp. gp. 1 fall within the encrusting growth-form categories (i.e. categories 6–9, text-fig. 18). It is worth emphasizing here the marked preference of *F.* sp. gp. 1 for occurrence in the C horizon, and its predilection for small colony size. Its occurrence in the B horizon is essentially limited to a series of small domes (text-fig. 18), and throughout the entire study area only two large B horizon colonies of *Favia* were recorded (text-fig. 18).

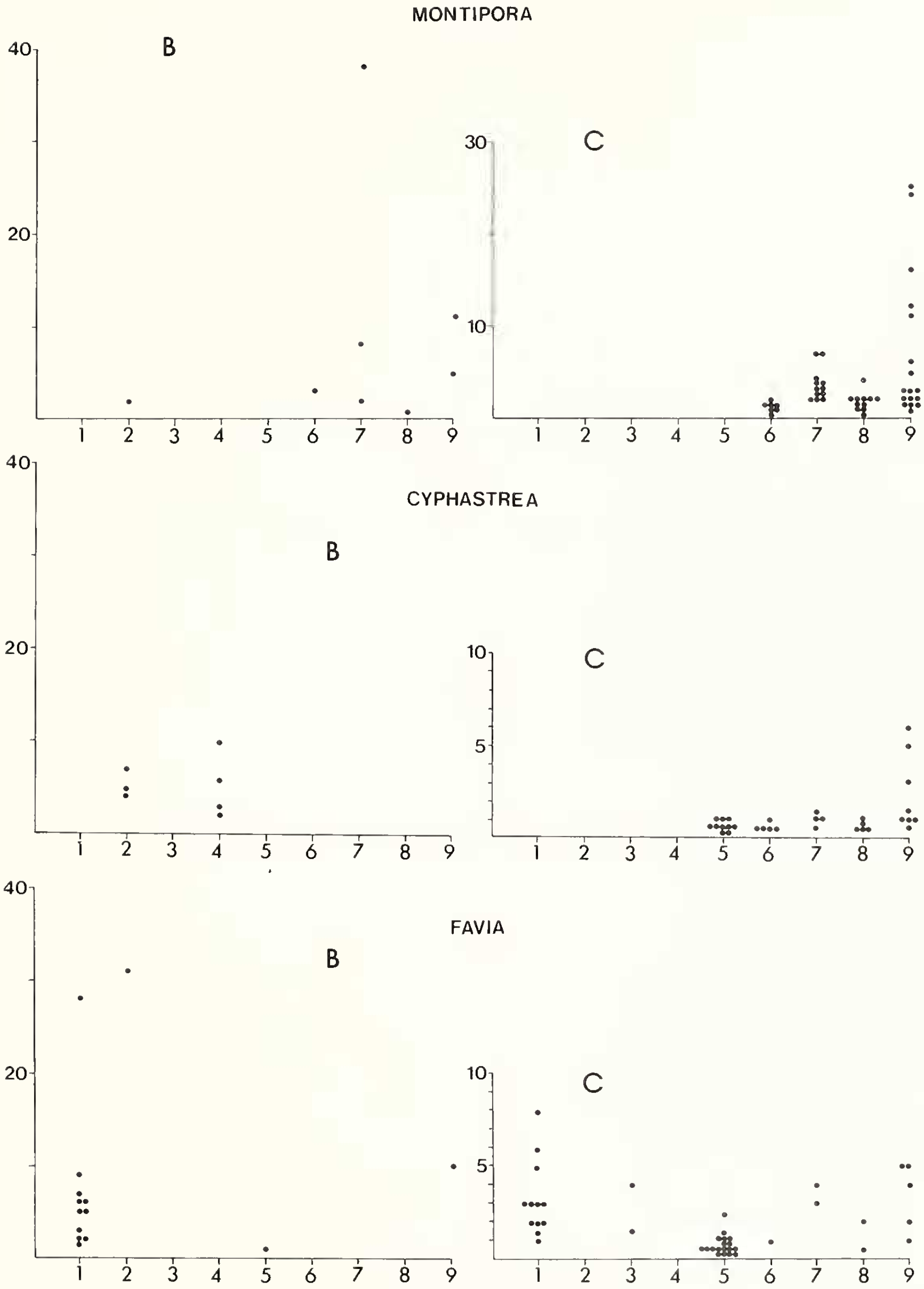
Echinopora occurs in approximately equal numbers of colonies in both the B and C horizons, but is almost exclusively confined to the platy-encrusting growth-form categories (i.e. categories 6 and 7, text-fig. 19). This suggests that although *Echinopora* may not have been selective in terms of the type of substrate it colonized, it was in terms of the growth form that it always (or nearly always) adopted. A similar trend is suggested for *Goniastrea*, which shows some preference for occurring in the B horizon as domes formed out of encrusting layers (category 2) and in the C horizon as thick doming-encrusting colonies (category 9) (which is a not dissimilar growth form) (text-figs. 3 and 19). However, this trend is complicated by the occurrence of a number of very small colonies of *Goniastrea* in several other growth-form categories (text-fig. 19). It may be that adult colonies of *Goniastrea* are consistently dome-shaped, but more data are required before such a trend can be verified.



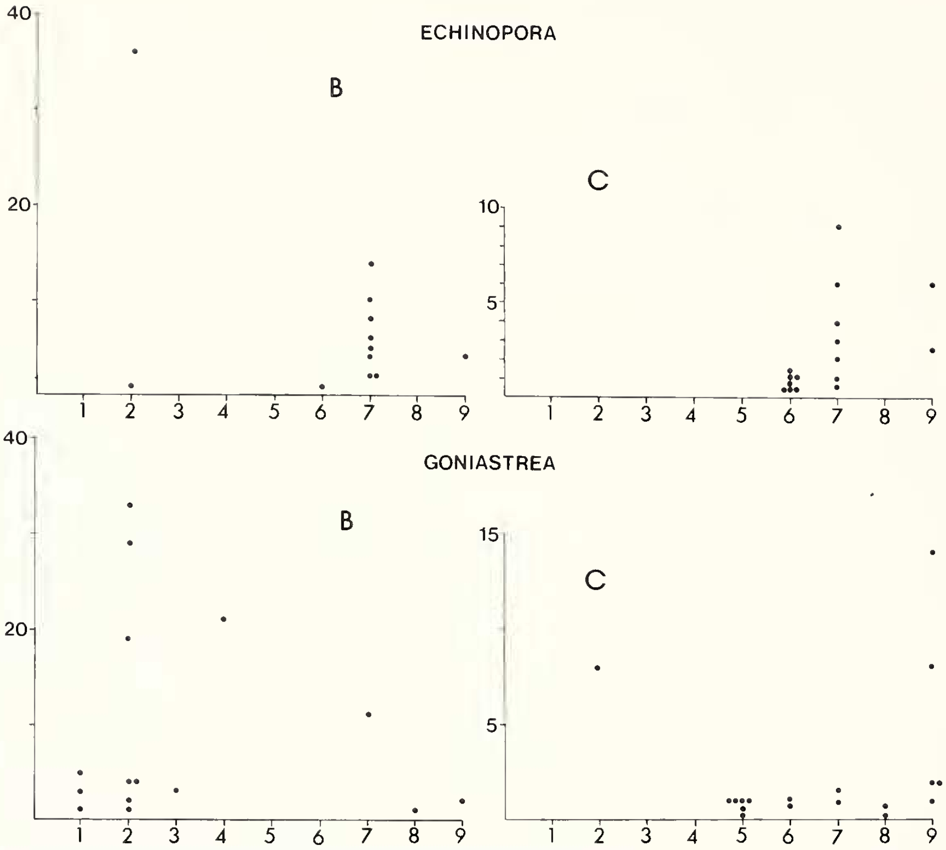
TEXT-FIG. 17. The structural roles adopted by three corals with predominantly B horizon strategies. The graphs plot the importance values (ordinate) against the growth forms (abscissa) for each individual colony in both the B and C horizons (pooled data from the three areas investigated). The nine growth-form categories are those defined in text-fig. 3. Coral groupings: *Platygyra* (= *P. lamellina* + *P.* sp.); *Leptastrea* (= *L.* sp. gp. 1 + *L.* sp. gp. 2 + cf. *L.* sp. gp. 1 + cf. *L.* sp. gp. 2).

Corals, habitat strategies and resource partitioning

The evidence presented above strongly suggests that the principal coral types present in the back-reef patches of the Kenya Pleistocene reef adopted distinct habitat strategies, for they appear to be consistently grouped into certain three-dimensional growth-form categories within either B or C horizons. More data are required to fully substantiate these trends, but it would appear from evidence such as this that many coral types may well be much more specific in their habitat resource requirements than has previously been recognized. If this is indeed the case, it could be argued that



TEXT-FIG. 18. The structural roles adopted by three corals with predominantly C horizon strategies. The graphs plot the importance values (ordinate) against the growth form (abscissa) for each individual colony in both the B and C horizons (pooled data from the three areas investigated). The nine growth-form categories are those defined in text-fig. 3. Coral groupings: *Montipora* (= *M.* sp. + cf. *M.* sp.); *Cyphastrea* (= *C. micropthalma* + *C.* sp. + cf. *C.* sp.); *Favia* (= *F.* sp. gp. 1 + cf. *F.* sp. gp. 1).



TEXT-FIG. 19. The structural roles adopted by two corals with approximately equal preference for both the B and C horizons. The graphs plot the importance value (ordinate) against the growth form (abscissa) for each individual colony in both the B and C horizons (pooled data from the three areas investigated). The nine growth-form categories are those defined in text-fig. 3. Coral groupings: *Echinopora* (= *E. gemmacea* + *E.* sp.); *Goniastrea* (= *G. retiformis* + *G. pectinata* + *G. incrustans* + *G.* sp.).

here is direct evidence that corals have effectively partitioned at least part of the available habitat space on patch reefs. As a direct result of interspecific competition for the occupancy of this space, each of the principal component species has evolved a distinct habitat strategy.

There is a certain amount of both theoretical and empirical evidence to support the contention that competition for the occupancy of space is a fundamental determinant of community structure in all sessile communities (see e.g. Yodzis 1978). Furthermore, it is likely that such competition will be particularly intense on coral reefs, where a whole host of sessile organisms vie for the occupancy of a limited substrate area (e.g. Porter 1976, p. 732; Wijsman-Best 1977, p. 472; Buss 1979, p. 475). In the face of such strong competition it would seem reasonable to suppose that corals had finely partitioned the habitat resources available to them, with each species (or at least each of the common species groups) evolving a morphological strategy that allowed them to occupy a unique portion of the available habitat space. Much of the structure seen in both recent and fossil coral communities must be due to corals adopting a variety of distinct habitat strategies. The importance of habitat resource partitioning in all types of plant and animal community has been strongly emphasized by Schoener (1974).

As it has also been argued that corals have partitioned their trophic resources (adopting a variety of strategies between the extremes of autotrophy and heterotrophy—Porter 1976), it might seem that they have in fact achieved a degree of resource specialization equivalent to that attributed to many groups of reef-dwelling invertebrates. Might not corals be as specialized in their habitat and trophic requirements as, for example, predatory reef gastropods (see, for example, Kohn 1971; Leviten 1978; Taylor 1978*a*)? Until recently, the prevalent view among ecologists has been that reef communities are the epitome of complex, co-evolved species assemblages in which the available resources have been repeatedly subdivided by a continual process of interspecific competition and niche partitioning. The very high species diversities observed on reefs are held to be the product of fine scale partitioning in (supposedly) benign tropical environments (lucidly reviewed in Hutchinson 1978). Such explanations are persuasive when applied to motile reef-associated organisms such as predatory gastropods, but it can be questioned whether they apply to the corals themselves. It has recently been argued (notably by Connell 1978) that corals are very generalized in their use of resources. Although they derive some of their energy requirements from ingested zooplankton, much undoubtedly comes from the photosynthesis of their symbiotic zooxanthellae, and they may be almost as generalized in their trophic requirements as the analogous trees in a tropical rain forest. There may well have been some differentiation along a trophic resource axis from autotrophy to heterotrophy (Porter 1976), but Connell (1978) believes that this has contributed little to the coexistence of closely related species. Vertical stratification, with autotrophs above heterotrophs, has yet to be convincingly demonstrated on a recent reef, and there is no indication that heterotrophs become proportionately more important constituents of the poorly lit deeper-water coral assemblages. Connell also argues that corals are generalized along the habitat niche axis: although known to occur on reefs within well-defined zoned assemblages (e.g. Lang 1974; Rosen 1975), there is (as yet) little indication that individual coral species are restricted in their distribution within these zones (e.g. Goreau 1959; Stoddart 1969; Loya and Slobodkin 1971; Rosen 1975, 1977). Connell (1978, p. 1309) considers it unlikely that corals could have partitioned the available spatial and trophic resources on reefs to the extent necessary to account for some of the very high observed diversities within coral assemblages.

There has always been a certain element of conjecture associated with the 'niche-partitioning' diversity model, for there is often no direct evidence to show precisely which resources may have been competed for or how exclusion actually occurred. It is probably true to say that the process of competitive exclusion has more often been inferred than demonstrated, and in nearly all groups of organisms remains poorly understood. In addition, there has always been a small but persistent flow of data to suggest that some species with apparently identical resource requirements can coexist indefinitely (see, for example, Sale 1974; Birch 1979). How can facts such as these be reconciled with a theory which states that at equilibrium each species within a community must occupy some unique share of the resource spectrum? The answer to this question probably lies in recent suggestions that many (perhaps all) communities may not, after all, exist in a state of equilibrium. Connell (1975, 1978), for example, has suggested that species population densities are seldom great enough for actual competition for resources to occur: natural disturbances (such as storms or plagues of predators or pathogens on reefs) continually affect all communities, and it is likely that they do so at a rate greater than the intrinsic rate of natural recovery. Disturbances may be so frequent that equilibrium conditions are never attained on reefs (see, for example, Sale 1977; Endean 1977; Connell 1978; Taylor 1978*b*). Huston (1979) has suggested that a crucial factor determining the species diversity of a community may be the *rate* at which the component species approach competitive equilibrium. Under non-equilibrium conditions there would appear to be a dynamic balance between the rate of competitive exclusion and the disruptive forces that prevent equilibrium being attained. If, for example, there were rapid rates of intrinsic natural increase amongst the component species, the dominant species would rapidly become commonest and an equilibrium state would be quickly attained. If, on the other hand, the component species had slower rates of natural increase, then the dominant species would take longer to dominate and there would be a slower approach to equilibrium. In other words, an increase in population growth rates would tend to reduce species diversity, and a decrease would tend to increase it. Connell (1978, p. 1309) has stressed that the problem of overlap between species with apparently similar resource requirements is removed if non-equilibrium conditions are assumed.

We are left then, with two equally compelling models of coral community structure: one based on equilibrium conditions (the niche-partitioning model) and the other on the existence of non-equilibrium conditions. If perhaps the weight of theoretical evidence favours the former, then the weight of empirical data (to date) tends to favour the latter. It must be emphasized, however, that much more detailed information on the resource requirements of scleractinian corals is required to fully substantiate the claims of either model. It is important to emphasize too, that the non-equilibrium model deals primarily with the maintenance rather than the generation of diversity (Huston 1979, p. 81). It is possible that over evolutionary rather than ecological time, corals could have partitioned (through a process of interspecific competition and competitive exclusion) at least some of the available resources on reefs. There is now evidence to suggest that a number of common coral species may be restricted to comparatively narrow depth zones (e.g. Dinesen 1977), and the present study indicates that they may also be confined to distinct growth-form and substrate types. Certain corals consistently colonized soft substrates and others hard substrates; some are typically doming and massive in form and others are thin and encrusting (and there are, of course, many other growth-form types). These occurrences of corals in distinctive three-dimensional growth forms, on certain types of substrate and within certain depth ranges, can all be taken as evidence of partitioning of at least part of the available habitat space on reefs. Many of the common coral species (and especially those occurring in back-reef patches) have apparently evolved distinct habitat niches. However, whether the extent of the ecological separation that this habitat partitioning provides is sufficient to permit species with otherwise identical resource requirements to coexist has yet to be determined. It has been suggested (Rosen 1981) that the occurrence of corals in distinct strata (or horizons) may also be a by-product of some form of trophic resource specialization, for if the same species consistently adopt the same positions and attitudes on a reef edge then they may well have been able to effectively partition both the incident light energy and the water currents bearing zooplankton. Perhaps the nature and extent of resource partitioning in scleractinian corals will only be fully resolved by a combination of studies on fossil and living reefs.

CONCLUSIONS

The process of ecological succession on small patch reef structures can be studied by employing the concept of ecological stratification. In fossil patch reef studies this involves mapping vertical sections through patches in detail and assigning the component corals to either of two basic categories, the B or C horizons (or strata). B horizon corals are the pioneers that colonized soft substrates, and C horizon corals are later colonizers on top of the initial B's. The potential exists for this technique to be considerably refined and extended: in particular, it should be possible to study the later stages of succession by finely subdividing the C horizon. Patch reefs throughout the geological record are amenable to stratification analysis.

Small patches are particularly well exposed in the Pleistocene reef limestones of the Kenya coast. Most of the present-day exposures are through what were extensive back-reef facies, and it is clear that patches thrived in conditions varying from very shallow water (intertidal in places) to deep water (i.e. 10 m+). Available evidence suggests that the greatest amount of stratification occurred in the deeper-water areas, where there were conditions of increased fine sedimentation and periodic rubble incursions. The small size of so many of the patches can probably be linked to the existence of comparatively shallow-water conditions over much of the back-reef region.

Whereas B horizon corals are typically medium to large in size and have doming and massive growth forms, C horizon corals are much smaller and generally have encrusting growth forms. The commonest B horizon coral is *Porites* sp. gp. 2, which occurred throughout the back-reef region in a variety of environments and clearly played a fundamental role in patch reef formation. Massive faviids, such as *Platygyra* and *Leptastrea*, are much less prominent as pioneers. The mussids *Galaxea fascicularis* and *Lobophyllia* are both essentially restricted to the B horizon, but only occasionally supported any significant stratification. The three commonest C horizon corals are, encrusting *Montipora* (in more open-water areas), encrusting *Cyphastrea* (in quieter, deeper-water areas), and massive *Favia* (in the form of small domes and encrusting patches).

Certain corals may be much more specialized in their habitat requirements than has previously been recognized. In the back-reef patches of the Kenya Pleistocene reef the principal coral types consistently adopt distinctive three-dimensional growth forms within either the B or C horizons. *Porites* sp. gp. 2 and *Platygyra* occur over a wide size range within the doming-massive growth-form category of the B horizon and *Cyphastrea* and *Montipora* in small size classes within encrusting growth-form categories of the C horizon. Although these latter two corals have very similar growth forms, they do not co-occur extensively on the reef. The third common C horizon coral, *Favia*, has a very distinctive growth form of small domes and tiny encrusting patches. *Echinopora* and *Goniastrea* show no apparent preference for either the B or C horizons, but there is evidence to suggest that they consistently occur in the same three-dimensional form.

It can be argued that the principal coral types in the back-reef patches of the Kenya Pleistocene reef have effectively partitioned at least part of the available habitat space. More information is required to fully substantiate the trends observed in this study, but it would appear that analysis of the sequential development of fossil patch reefs may yield important new evidence as to the habitat specificity of scleractinian corals. Such evidence is likely to prove of considerable importance in determining whether coral communities have evolved under essentially equilibrium or non-equilibrium conditions.

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